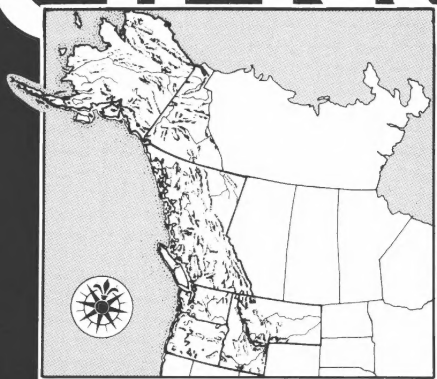


February 1993

Volume 67, Number 1

BALD EAGLE
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NORTHWEST SCIENCE



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(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

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David L. Peterson
College of Forest Resources
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Announcements

1993 Annual Meeting of the Northwest Scientific Association

The Northwest Scientific Association will hold its 66th Annual Meeting on March 25-27 at Eastern Oregon State College, La Grande, Oregon. Symposium topics will include "Research and Management of Bats in the Northwest," "Cumulative Effects of Land Management Practices on Anadromous Salmonids," and "Status of Forest Health Issues in Northeast Oregon." Contributed paper sessions will occur in the areas of Botany, Forestry, Geology, Range Science, Aquatic Ecology, and Zoology. The banquet speaker (March 25) will be Jack Ward Thomas. A juried show of wildlife art will be open throughout the meeting.

Northeast Oregon offers a rich diversity of ecosystems, and field trips will be scheduled to take advantage of this. Field trips may also supplement the symposia.

The deadline for abstract submission is February 1, 1993. A program listing paper titles, authors, and scheduled times will be mailed to members in early March. Abstracts will be available at the meeting and will be published in the May issue of *Northwest Science*. Students are strongly encouraged to participate.

For additional information regarding the meeting, contact Dr. Karen Antell, Program Chairwoman, or Dr. Burr Betts, NSA President, Biology Department, Eastern Oregon State College, La Grande, OR 97850-2899; (phones: 503-962-3610 and 503-962-3330, respectively).

1993 Student Research Grant

I. ELIGIBILITY

Applicants must be regular members of the Northwest Scientific Association. *Northwest Science* (the journal of the society) has information for joining the society.

II. PREPARATION OF THE PROPOSAL

A cover page should be provided to include: Name and address of applicant, associated institution, name of major professor/advisor, degree program, year in school, and amount of money requested (maximum of \$500).

The proposal should include: Title, Statement of Justification, Methodology/Experimental Design (including methods of analysis), and detailed budget (on separate page).

The proposal length should be no more than three (3) *double spaced* pages (not including budget page).

Proposals are due on or before **MARCH 1, 1993** and should be sent to:

Dr. R. Gerald Wright
Department of Wildlife Resources
University of Idaho
Moscow, ID 83843
Phone (208) 885-7990

Grants will be awarded at the annual meeting of the Northwest Scientific Association held in La Grande, Oregon, March 24-26, 1993.

Awards provided by the Northwest Scientific Association are designed to help students complete research projects in the basic and applied sciences and social sciences. Monies should be used only to support research activities of the student. It is expected that students will report results of their research at a future NSA meeting.

A Message from the Editor

A large fraction of the Pacific Northwest is comprised of public lands, encompassing large tracts of federal, provincial, territorial, and state ownerships. As a result, there is probably no region of North America where there are as many challenging issues in resource management. Some of these issues are prominently displayed in newspaper articles and television throughout Canada and the United States, as well as in the international media. Yes, the world is now truly aware of the beauty, resources, and problems of the Pacific Northwest.

Much of this recent notoriety is the result of controversies surrounding forest resource management and the northern spotted owl. But there are many other issues that have taken center stage as well: water supplies, anadromous fisheries, the rights of indigenous peoples. Each natural resource issue is intrinsically linked to social and economic issues relevant to local and regional human impacts. All these topics—in the basic and applied sciences—are what *Northwest Science* is all about.

Scientists need to step into the chaotic environmental arena and act as a positive force for change. Everyone has something to offer. Biologists need to provide us with a better fundamental understanding of the ecological characteristics of natural resources. Physical scientists can describe interactions between climate and the physical landscape. Engineers can provide us with technological information that will lead to solutions to environmental problems. Social scientists and anthropologists can help integrate the human element (past and present) into natural resource issues. We need this sort of interdisciplinary effort in order for scientists to have an impact on societal problems.

Given this background, I find it a particularly exciting time to assume the editorship of *Northwest Science*. I look forward to the journal having an increasing impact in the field of natural resources by continuing to provide high quality scientific information in a wide range of disciplines. I would encourage authors to consider the broader impacts of their studies, as well as regional implications. Perhaps the phrase "Think globally, act locally," is appropriate here. *Northwest Science* is read by scientists throughout North America and in many international libraries—the Pacific Northwest has a lot to offer the scientific world.

I encourage you to submit your best work to *Northwest Science*. I also encourage you to participate in the Northwest Scientific Association, attend the annual meeting, and get students involved. Above all, however, I urge everyone to just *get involved* in whatever issues are important to you as a scientist and citizen. As someone once said, "ninety percent of life is just showing up."

As new editor of *Northwest Science*, I will strive to maintain the high quality on which previous editor Ken Kardong insisted. Ken's editorship produced excellent issues of *Northwest Science* for six years; I am indebted to him for sharing his experience with me during the editorial transition. I would also value the ideas and comments of our readership—please feel free to contact me about any matters concerning *Northwest Science*. I look forward to working with you!

David L. Peterson
Cooperative Park Studies Unit
College of Forest Resources
University of Washington, AR-10
Seattle, WA 98195 (USA)

Telephone: 206-543-1587
Fax: 206-685-0790
Internet: wild@u.washington.edu

Rainfall Induced Changes in Chemistry of a British Columbia Coastal Stream

Abstract

A small coastal stream in British Columbia was sampled during two storm events to measure stream chemistry changes. Samples were collected at 30 minute intervals throughout the storms to assess changes in stream chemistry on a temporal basis. During rain events, streamwater showed a decrease in chloride, nitrate, and sulphate concentrations. Stream pH decreased by 0.3 units during these events while the buffering capacity, measured as alkalinity, appeared to be consumed in addition to dilution effects. After the storms, stream chemistry tended to slowly return to the pre-storm conditions over a period of several days. Results showed that rainstorms drive marked chemical changes on a scale of hours.

Introduction

The objective of our study was to identify some of the changes in stream chemistry in Kanaka Creek, a small coastal stream in which rain driven pH depressions had previously been observed (Whitfield and Dalley 1987, Whitfield and Wade 1991). Rainfall events affect water chemistry in small streams (Corbett and Lynch 1982, Lynch *et al.* 1986, Whitfield and Dalley 1987, Muraoka and Hirata 1988) and rivers (Byrd, 1990). Each rain event and its effects on stream chemistry can be unique (Whitfield and Dalley 1987).

In a complex watershed, such as Kanaka Creek, many processes take place simultaneously. Direct and indirect effects of urbanization have the potential to change the existing ecosystems. Understanding the processes presently operating in such watersheds, and the scales at which they take place, is critical to the prediction of future impacts. Processes may be impacted in several ways as human activity increases both within and around the watershed. We may see changes in the inputs of materials, the structure of hydrologic events, and in the forest ecosystem within the watershed.

Most studies of acidification have been in Scandinavia and Eastern North America, while the west coast of North America has been less studied. These coastal areas are characteristically sensitive to acidic inputs and receive large amounts of rainfall (Swain 1987; Driscoll *et al.* 1988). In or near urban areas, local emissions of acid precursors can acidify precipitation. The water courses near

Vancouver, British Columbia, are particularly at risk due to their low buffering capacity and to significant atmospheric inputs from local sources. Rain pH values of 4.7 to 5.4 have been reported for the Vancouver area (Zeman and Slaymaker 1978, Nikleva 1985). Nikleva (1985) indicated that lower pH levels observed downwind of Vancouver, in areas such as Kanaka Creek, were consistent with an urban impact.

Streamwater chemistry was observed over a two year period and during four rainfall events in a forested basin in Japan by Muraoka and Hirata (1988). During rainfall events, water chemistry variables decreased due to dilution by surface runoff water until peak flow. In the recession period two major modes were observed: [1] some variables return to the same concentrations as before the event (elements which are minor or nonessential—specific conductance and chloride), and; [2] some variables overshoot the baseflow concentrations (elements essential to forest soil ecosystems—nitrate). Muraoka and Hirata (1988) suggest that in the recession period, the streamwater might be originating mainly from interflow associated with surface soil water rather than deep soil water.

Driscoll *et al.* (1988) report results from Jamieson Creek, a nearby watershed of similar attributes, although smaller in area and at higher elevation. Their study was spatial in nature and considered changes in stream chemistry with increasing elevation at one point in time. Their results from Jamieson Creek show that with increasing downstream distance, basic cation concentrations increased and DOC decreased, resulting in neutral pH values and positive alkalinity.

Current Addresses:

¹N. Rousseau—Environment Quebec, Ste. Foy, Quebec.

²E. Michnowsky—deceased December 1991.

Our study focuses on the temporal aspects of actual rainfall events. Rainfall events reduce stream pH and conductance (Whitfield and Dalley 1987, Whitfield and Wade 1991). Rainfall driven pH depressions are just one class of transient event which can be observed in small streams (Whitfield and Wade, 1991). We sought to gather detailed chemical data for a restricted set of variables on a scale appropriate for a temporal event. The pH values observed in a stream are the net result of a number of processes and reactions occurring before, during, and after rainfall. We present data demonstrating some chemical changes that occur in Kanaka Creek during rain events, with emphasis on those water quality variables related to stream pH. In particular, our results focus on acid related anions, pH, and the buffering capacity of the streamwater. Our specific questions were: [1] Is stream alkalinity reduced to a point where pH is driven by the pH of the rain? (i.e., the buffering capacity is exceeded); and [2] what changes in stream chemistry take place during a rain event?

Materials and Methods

The Kanaka Creek watershed is a minor tributary to the Fraser River (Figure 1). It drains an upland area of about 55 km². The basin has shallow soils and responds quickly to rainfall (Whitfield and Dalley 1987). The watershed is heavily forested in the northern portion, while the southern portion is lightly populated with small farms and residential areas. The monitoring site on Kanaka Creek is lo-

cated at a small salmon hatchery roughly six km from the mouth (Dalley 1986). This site represents a drainage area of 23 km² which has a mean annual flow of ± 1.4 m³/sec.

The data presented here were gathered during two storms. Samples were collected from the creek every 30 min. beginning at the start of the event. Rain samples were collected with a large polyethylene sampler as 30 min. composites, provided that sufficient rain fell in the interval. At the time of sampling gauge height was observed on a staff gauge, and subsequently converted into stream flow from a rating curve developed for this site. Measurements of stream pH and alkalinity, and rain pH and acidity were made on site within 30 minutes of collection using standard analytical and QA/QC methods (Environment Canada 1979). Acidity of the rain was determined using Gran's titration, and stream alkalinity was determined by a two point titration for low alkalinity determinations. Total acidity is expressed in mg/l as sulphate. The alkalinity of water is its acid-neutralizing capacity and is expressed in terms of calcium carbonate. Anions measured (Cl⁻, NO₃⁻, and SO₄⁼) were determined by ion chromatography. Cations were not measured in the present experiments.

Results

The temporal nature of the two storms is shown in Figures 2 and 3. Observed stream chemistry changes were quite similar in both storms, despite some differences between the two rain events. In

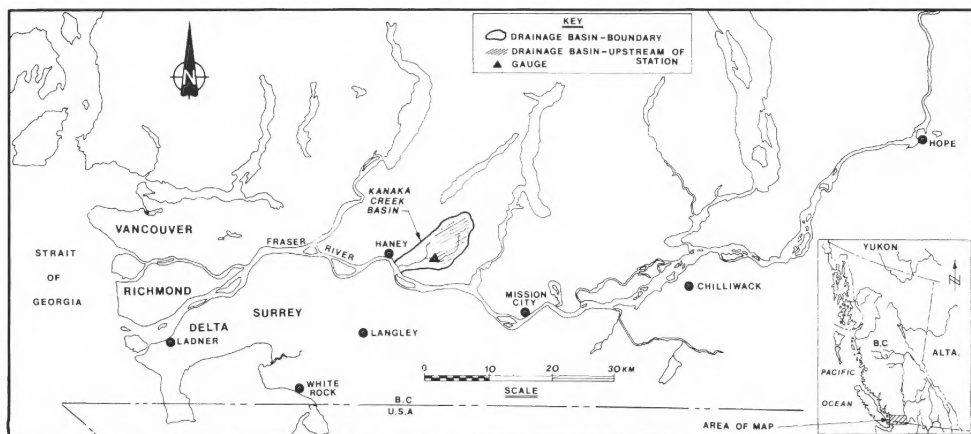


Figure 1. Kanaka Creek watershed and the location of the sampling site.

Kanaka Creek

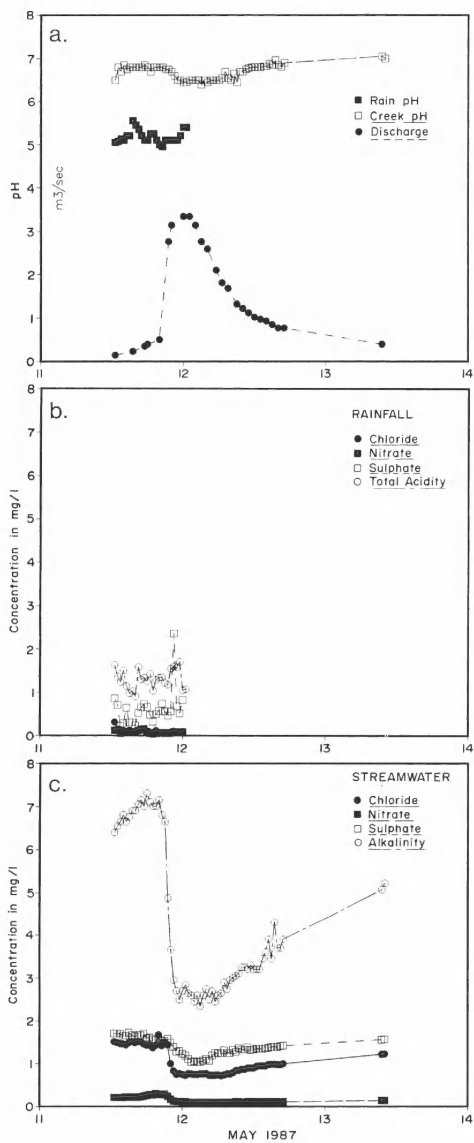


Figure 2. Measurements from rain event of May 1987. (a). Stream flow ($\text{m}^3\text{sec}^{-1}$), stream pH and rain pH; (b). Chloride, sulphate, nitrate, and total acidity measured in rainfall; (c). Chloride, sulphate, nitrate, and alkalinity measured in Kanaka Creek.

Kanaka Creek

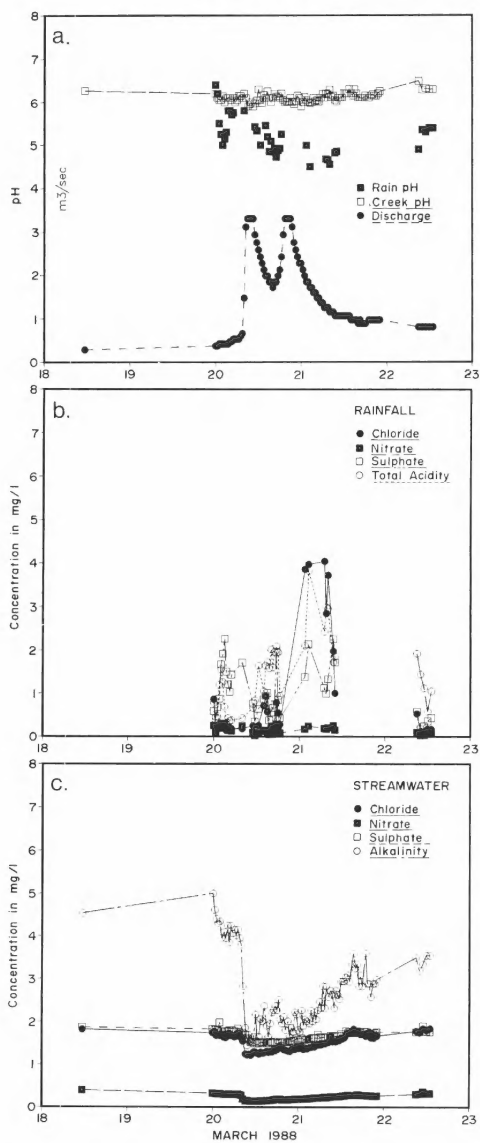


Figure 3. Measurements from rain event of March 1988. (a). Stream flow ($\text{m}^3\text{sec}^{-1}$), stream pH and rain pH; (b). Chloride, sulphate, nitrate, and total acidity measured in rainfall; (c). Chloride, sulphate, nitrate, and alkalinity measured in Kanaka Creek.

particular, concentration changes during the rising limb of the storm hydrograph show abrupt decreases with discharge increases and a smoother return to baseflow levels.

The first storm event occurred on 11-12 May 1987. Stream flow showed a large increase 6 hours after the onset of rain (Figure 2a). Rain pH during this event ranged from 4.95 to 5.5. Stream pH at the onset of the storm was about 6.7 and decreased to 6.4 at the same time as stream flow reached its maximum (Figure 2a). These lower pH values continued until the flow peak began to recede.

Rain chemistry during this event (Figure 2b) showed a very dilute rain. Sulphate levels were quite variable, ranging from a minimum of 0.23 to 0.82 mg/L, with one value of 2.36 mg/L. Chloride ranged from 0.05 to 0.31 mg/L, nitrate from 0.05 to 0.15 mg/L, and total acidity from 0.91 to 1.71 mg/L (Figure 2b). There did not appear to be any pattern to the chemistry of the rain during this event.

Concentrations of alkalinity, sulphate, chloride, and nitrate in streamwater decreased during the rain event (Figure 2c). Chloride concentrations decreased during the event from 1.5 to 0.7 mg/L, or roughly in half. Using chloride as a reference, sulphate did not become as dilute, decreasing from 1.7 to 1.0 mg/L (59%). The rate of change for sulphate was also much more gradual, chloride concentration changes occurring over two hours while sulphate concentration changes took about four hours. Nitrate concentrations changed from 0.21 to 0.11 mg/L (52%). The most dramatic change was observed for alkalinity. At the onset of the storm alkalinity was in the range 6.5 to 7.1 mg/L. In a two hour period alkalinity decreased from this level to 2.2 mg/L, about 34% of the initial level.

The second storm event was sampled on 20-21 March 1988. The lag between the onset of rainfall and increases in stream flow was about 8 hours (Figure 3a). This lag was longer than the previous event. Rain fell intermittently during this storm, with two main rainfall periods mixed with periods of light drizzle. Stream flow generated by this storm had two corresponding peaks (Figure 3a). Rain pH values ranged from a low of 4.5 to a high of 6.4. The highest rain pH values were in the range from 6.2 to 5.9, and again, lowest stream pH values occurred at peak stream flows.

The chemistry of the rain during the March 1988 event was highly variable (Figure 3b). Sulphate concentrations were very variable, ranging from 0.56 to 2.26 mg/L. Chloride concentrations were quite low during the early portion of the event (0.2 to 0.9 mg/L) and then increased to high levels in the late stages of the storm (4.0 mg/L). Nitrate concentrations were in the range 0.10-0.25 throughout the storm. Total acidity also had low concentrations (0.5-1.6 mg/L) at the beginning of the storm and higher concentrations (2.1-3.8 mg/L) during the late stages of the storm (Figure 3b).

Similar to the May 1987 event, the concentration of ions in streamwater was strongly affected by the rainfall event. Chloride concentrations were reduced from an initial concentration of 1.8 mg/L to a low concentration of 1.3 mg/L, 72% of the initial values (Figure 3c). This change in concentration occurred over a period of less than two hours. Sulphate concentrations also decreased, from about 1.9 to 1.5 (79%). This was substantially less of a decrease than for chloride, and, as with the May 87 event, the rate of change was much slower than chloride, taking about four hours. Nitrate concentration changes were similar to the earlier event from an initial concentration of about 0.32 to a minimum of 0.17 mg/L. Alkalinity again showed the most dramatic change in concentration, decreasing from an initial value of about 4.5 to a low of 1.4 mg/L. This change was very rapid, taking only two hours to change by more than 3 mg/L. Alkalinity concentration at the lowest values was about 30% of the initial value. Stream flow demonstrated two distinct peaks during this event (Figure 3a). Stream chemistry changes show patterns dominated by the effects of first flow peak. The impact of the second flow peak is minor compared to the first peak. Most evident among the changes accompanying this second peak in flow is a slight decrease in alkalinity (about 0.4 mg/L).

Discussion

While only the two rain events were observed in the present study, the changes in stream chemistry during both events were quite similar. Stream flow increases did not occur for several hours after the onset of rain. Significant changes in stream chemistry lagged behind flow increases by one to two hours. Changes in alkalinity, when they did occur, took place very rapidly, reaching minimum

values in one to two hours after change was first observed. Multiple rain events, such as the one observed in March 1988, generated an initial and a secondary decrease in alkalinity.

Rain-induced changes in pH and specific conductance on the scale of hours in the Kanaka Creek watershed were observed by Dalley (1986) and Whitfield and Dalley (1987). The results presented here show that while stream chemistry changes during storms, stream pH may not be greatly affected. Whitfield and Dalley (1987) noted that not all storms affecting Kanaka Creek produce significant depressions in pH.

Our results were generally consistent with those of Muraoka and Hirata (1988), except that nitrate concentrations did not overshoot the baseflow concentrations during the recession periods as in their study. This difference is likely due to the poor soil development within the Kanaka Creek watershed. The recession periods in Kanaka Creek were longer in duration than those reported by Muraoka and Hirata (1988).

Rainfall driven events exist for only short periods of time. In areas such as the west coast of North America where stream flow is controlled by rainfall rather than snow accumulations, these transient events may have significant environmental consequences. Muraoka and Hirata (1988) show that more variation in stream chemistry occurred during rain events than was observed in two years of biweekly sampling. In the Kanaka Creek watershed, the increasing impact of human activities over time may have changed the manner in which the stream responds to rainfall.

Stream chemistry does not appear to be directly related to rain chemistry. The rain of the May 1987 event was very dilute yet had about the same effect on stream chemistry as the March 1988 event. Sulphate, chloride and nitrate concentrations were higher in streamwater than in the rain. The only period in which rain was higher in concentration for these was during a light rain episode at the end of the March 1988 event (Figure 3b). These concentrations of ions in rain are typical of those reported in Alaska and Oregon by Bormann *et al.* (1989). The lack of a relationship between stream chemistry and rain chemistry suggests that soil water and groundwater control stream chemistry. These results agree with findings for snow melt events (Peters and Driscoll 1987) and rain events (Kennedy *et al.* 1986).

Several processes are taking place in the Kanaka Creek watershed. Much of the observed variation can be accounted for by simple dilution associated with the flow increases caused by the events. Our results are consistent with subsurface flow dominating the storm hydrograph (Dunne 1983, Price and Hendrie 1983), rather than overland flow. Sklash *et al.* (1986) and Pearce *et al.* (1986) describe similar results occurring when "old" water is displaced by "new" water during a storm event. This process would account in part for the differences between rainfall and stream chemistry. It would also be consistent with the rapid rate of change in concentration we observed for the variables we measured.

Alkalinity was markedly affected during rainstorms, being reduced to concentrations below those expected from dilution alone. Alkalinity will be consumed through the neutralization of acidity. Driscoll *et al.* (1988) indicate that in Jamieson Creek the acidity present is largely due to weak organic acids. Weak organic acids are likely a major contributor to the existing acidity in the Kanaka Creek watershed. Our measurements show the presence of strong acids in the rainfall. Muraoka and Hirata (1988) identify the importance of surface soil water in this introduction of nitrate into stream flow. The alkalinity results we present suggest we consider a two source structure, surface soil water containing weak organic acids forming a significant component of the runoff after the onset period and a baseflow component of groundwater which contributed buffering capacity. Thus, during a rainstorm there would be a dilution effect due to the increase in runoff coupled with a soil water contribution of weak acids.

In both the events reported here, some residual alkalinity persisted. We anticipate that pH might be strongly affected if the residual alkalinity were to reach zero during a storm event. Such a situation might develop if acid inputs to the system were to increase, or if the baseflow, high alkalinity, component of the runoff decreased by reducing the infiltration of surface water. The continuing urbanization of the lower Fraser Valley of British Columbia may cause both these types of changes in watersheds like Kanaka Creek.

Conclusions

The transient nature of stream chemistry during rainfall events in a small coastal watershed was

demonstrated. Hydrologic and chemical changes in Kanaka Creek occur rapidly in response to rainfall events, but not exactly in phase. Dominating the observed transient changes is a dilution effect associated with increased streamflow. This effect

accounts for many of the concentration changes for the variables we observed; however, the buffering capacity of this stream was both diluted and consumed during rain events.

Literature Cited

- Bormann, B. T., R. F. Tarrant, M. H. McClelland, and T. Savage. 1989. Chemistry of rainwater and cloud water at remote sites in Alaska and Oregon. *J. Environ. Qual.* 18:149-152.
- Byrd, J. T. 1990. Riverine inputs in marine environmental quality monitoring. *In* L. Harding (ed.) *Monitoring Status and Trends in Marine Environmental Quality*. Environment Canada. Pp. 125-126.
- Corbett, C. S. and J. A. Lynch. 1982. Rapid fluctuations in streamflow pH and associated water quality parameters during a rainstorm. *In* A. I. Johnson and R. A. Clark (eds.) *International Symposium on Hydrometeorology*. American Water Resources Association. Pp. 461-464.
- Dalley, N. E. 1986. High frequency water quality monitoring of a coastal stream. *In* A. H. El-Shaarawi and R. E. Kwiatkowski (eds.) *Statistical Aspects of Water Quality Monitoring*. Pp. 433-442.
- Driscoll, C. T., N. M. Johnson, G. E. Likens, and M. C. Feller. 1988. Effects of acidic deposition on the chemistry of headwater streams: A comparison between Hubbard Brook, New Hampshire, and Jamieson Creek, British Columbia. *Water Res. Res.* 24:195-200.
- Dunne, T. 1983. Relation of field studies and modeling in the prediction of storm runoff. *J. Hydrol.* 65:25-48.
- Environment Canada. 1979. *Analytical Methods Manual*. Inland Water Directorate, Ottawa.
- Kennedy, V. C., C. Kendall, G. W. Zellweger, T. A. Wyerman, and R. J. Avanzino. 1986. Determination of the components of streamflow using water chemistry and environmental isotopes, Mattole River basin, California. *J. Hydrol.* 84:107-140.
- Lynch, J. A., C. M. Hanna, and C. S. Corbett. 1986. Predicting pH, alkalinity, and total acidity in stream water during episodic events. *Water Res. Res.* 22:905-912.
- Muraoka, K., and T. Hirata. 1988. Streamwater chemistry during rainfall events in a forested basin. *J. Hydrol.* 102:235-253.
- Nikleva, S. 1985. Acid rain over southwestern British Columbia. *In* J. H. Baldwin (ed.) *Proceedings of the Acid Rain Symposium*. Annual Conference of the Northwest Association for Environmental Studies. University of Victoria. Pp. 15-29.
- Pearce, A. J., M. K. Stewart, and M. G. Sklash. 1986. Storm runoff generation in humid headwater catchments 1. Where does the water come from? *Water Res. Res.* 22:1263-1272.
- Peters, N. E., and C. T. Driscoll. 1987. Sources of acidity during snowmelt at a forested site in the west-central Adirondack Mountains, New York. *In* R. H. Swanson, P. Y. Bernier, and P. D. Woodward (ed.) *Forest Hydrology and Watershed Management*. IAHS-AISH Publ. no. 167. Pp. 99-108.
- Price, A. C., and L. K. Hendrie. 1983. Water motion in deciduous forest during snowmelt. *J. Hydrol.* 64:339-356.
- Sklash, M. F., M. K. Stewart, and A. J. Pearce. 1986. Storm runoff generation in humid headwater catchments 2. A case study of hillslope and low-order stream response. *Water Res. Res.* 22:1273-1282.
- Swain, L. G. 1987. *Second Report on Chemical Sensitivity of B.C. Lakes to Acidic Inputs*. Ministry of Environment and Parks, Province of British Columbia. 31 pp.
- Whitfield, P. H., and N. Dalley. 1987. Rainfall driven pH depressions in a British Columbia coastal stream. *In* S. J. Nix (ed.) *Symposium on Monitoring, Modeling, and Mediating Water Quality*. American Water Resources Association. Pp. 285-294.
- Whitfield, P. H., and N. L. Wade. 1991. Monitoring transient water quality events using electronic data acquisition. *In* H. McWreath (ed.) *Water Management of River Systems*. American Water Resources Association. Pp. 311-312.
- Zeman, L. J., and H. O. Slaymaker. 1978. Mass balance model for calculation of ionic input loads in atmospheric fallout and discharge from a mountainous basin. *Hydrol. Sci.* 23:103-117.

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William C. McComb, Kevin McGarigal, Department of Forest Science, Oregon State University, Corvallis, Oregon 97331, and

Robert G. Anthony, U.S. Fish and Wildlife Service, Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, Oregon 97331

Small Mammal and Amphibian Abundance in Streamside and Upslope Habitats of Mature Douglas-fir Stands, Western Oregon

Abstract

Capture rates of small mammals and amphibians were compared between streamside and upslope habitats along 700-m transects in each of six mature Douglas-fir stands, 1988. Equitability and diversity of small mammal communities were higher along streamside than upslope transects. There was no difference in small mammal or amphibian species richness per transect between streamside and upslope transects. Community similarity between streamside and upslope habitats was <55 percent for both amphibians and mammals. Capture rates of marsh shrews (*Sorex bendirii*), Pacific jumping mice (*Zapus trinotatus*), long-tailed voles (*Microtus longicaudus*), white-footed voles (*Phenacomys albipes*), and Dunn's salamanders (*Plethodon dunni*) were higher along streamside than upslope transects. Capture rates of western red-backed voles (*Clethrionomys californicus*), creeping voles (*M. oregoni*), Townsend's chipmunks (*Tamias townsendii*), Trowbridge's shrews (*S. trowbridgii*), and Ensatina salamanders (*Ensatina eschscholtzi*) were higher along upslope than streamside transects. Capture rates of marsh shrews, Pacific jumping mice, deer mice (*Peromyscus maniculatus*), shrew-moles (*Neurotrichus gibbsii*), and Pacific shrews (*S. pacificus*) decreased with distance from the stream along transriparian gradients. Capture rates of western red-backed voles increased with distance from the stream.

Introduction

The importance of streamside habitat to maintaining small mammal diversity and abundance has been documented in the Midwest (Geier and Best 1980), southwest Oregon (Cross 1985), and the Oregon Cascades (Anthony *et al.* 1987, Doyle 1990). Few studies have been conducted on either small mammals or amphibians in streamside areas of the Oregon Coast Range, despite the need for this information to meet guidelines established by the National Forest Management Act (NFMA) and the Oregon Forest Practices Act (OFPA). The OFPA protects riparian vegetation for anadromous fish along fish-bearing streams and reduces non-point source pollution (Brazier and Brown 1973). The effects of OFPA regulations on terrestrial vertebrates are unknown.

Johnson and Lowe (1985) considered the transriparian gradient to be a major factor influencing the biological diversity and structural complexity of riparian zones in the southwestern United States. The influence of the transriparian gradient on small mammal or amphibian communities in western coniferous forests is largely unknown.

Our objectives were to: 1) compare small mammal and amphibian community structure and relative abundance between streamside and upslope habitats in mature Douglas-fir stands, 2) describe patterns of small mammal and amphibian abun-

dances along 400-m transriparian gradients in these stands, and 3) describe habitat associations of small mammals and amphibians.

Study Area and Methods

The study was conducted in the Drift Creek drainage, Lincoln County, Oregon (123°60' long., 44°45' lat.). The drainage is 179 km², almost completely forested, and has a bimodal age distribution of forest stands. About 50 percent of the drainage contains 0- to 30-year-old forest stands that regenerated following timber harvest. The remainder is dominated by mature forests (120-140 years old) that regenerated after a series of fires in the mid-1800's. We sampled within six mature stands that were >80 ha each, and contained a second- or third-order stream (Brown 1985:201). Streams averaged 2.8 m wide (SE = 0.4, range 2-5) and drained an average of 197 ha (SE = 345, range 82-330) of land. These stands were dominated by Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*); other tree species included western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*) and bigleaf maple (*Acer macrophyllum*). Understory vegetation was dominated by salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), vine maple (*A. circinatum*), huckleberries (*Vaccinium* spp.), Oregon-grapes (*Berberis* spp.), stinking currant (*Ribes bracteosum*),

sword fern (*Polystichum munitum*), and devil's-club (*Oplodanax horridum*). Average weekly precipitation measured at a NOAA weather station in Tide-water, Oregon, 4-12 km south of the study sites was 3.6 cm (range = 0-9) during April-July (wet season) and 0.07 cm (range = 0-0.1) during August-October (dry season).

Animal and Habitat Sampling

Within each stand we established a 700-m streamside transect <10 m from the stream, a 700-m upslope transect (400 m upslope) parallel to the streamside transect, and two 400-m transriparian transects that connected the ends of the streamside and upslope transects. All sampling occurred >100 m from the periphery of each stand. Pitfall trap stations were established every 100 m along the streamside and upslope transects and every 50 m along the transriparian transects ($n = 180$ total stations). We subjectively placed two pitfall traps (double-deep No. 10 tin can) within 5 m of the station. Snap trap (Museum Special) stations were placed every 20 m along the streamside and upslope transects and every 10 m along the transriparian transects ($n = 960$ total stations) such that one out of five snap trap stations coincided with a pitfall station. Two traps were set at each snap trap station in the wet season (see below).

We sampled stands in random order between 3 May and 28 June (wet season) and between 8 September and 15 October (dry season), 1988. Sampling was conducted during periods when the influence of the stream on use of riparian habitat by vertebrates may have been high (dry season) or low (wet season). Sampling was initiated in a new stand every seven days during the wet season and every day during the dry season. Within each stand, we set and checked Museum Specials daily during the first five sampling days (9,600 trap nights [TN]); the pitfalls were opened and checked weekly for 30 consecutive days (10,800 TN/season). All animals were removed from the sites. Specimens of shrews were deposited in the National Museum, Washington, D.C.; all other taxa were stored as frozen specimens in the Department of Forest Science, Oregon State University. Snap trapping was abandoned in the dry season because pitfalls sampled all but two of the common species captured during the wet season (McComb *et al.* 1991). Patterns of capture rates were similar between the wet and dry seasons, so capture rates

were averaged between seasons and averages were used in subsequent statistical analyses.

We either directly measured or derived 39 habitat variables that described floristics and vegetation structure at 20-m radius plots centered on pitfall stations (Table 1). Field measurements were conducted from May-September, 1988. Captures of mammals in snap traps within 20 m of a pitfall station were assigned to that pitfall station for habitat analyses because habitat characteristics were only measured at pitfall stations.

Statistical Analyses

The total number of captures of each species at each trap station was determined and converted to capture rates (captures/1,000 TN). We tallied captures by species along streamside and upslope transects and calculated Shannon-Weaver species diversity ($H' = -\sum p_i \log p_i$), equitability ($E = H'_{\text{observed}}/H'_{\text{max}}$), and richness (number of species) for small mammal and amphibian communities (Brower and Zar 1984:157-160). We also calculated proportional community similarity (PS) between streamside and upslope transects (Brower and Zar 1984:161-164).

Analyses were conducted in three steps for each species: (1) comparison of capture rates and community structure between upslope and streamside transects, (2) association of capture rates with distance from water along the transriparian transects, and (3) identification of habitat variables that best separated capture sites from non-capture sites.

First, we tested the null hypothesis that capture rates did not differ ($P < 0.05$) between streamside ($n = 6$) and upslope transects ($n = 6$) with a Wilcoxon rank-sum test because data were not normally distributed.

Second, Pearson correlation coefficients of capture rates with linear and log-linear distances from the stream were used to assess transriparian patterns of relative abundance for species with $n \geq 20$ captures. Captures were pooled for each of the two sample points within each stand at each distance from the stream ($n = 54$).

Third, for species with ≥ 20 capture sites and ≥ 20 non-capture sites (10 species), we used stepwise discriminant function analysis (DFA) to select no more than six independent ($r < 0.80$) habitat characteristics that best separated capture sites from non-capture sites (Williams *et al.* 1990). Results are only reported for models with >80

TABLE 1. Habitat variables ($\bar{x}$, SE) along streamside ($n^a = 6$) and upslope ($n = 6$) transects in six mature Douglas-fir stands, 1988, Lincoln County, Oregon.

Habitat characteristic	Streamside	Upslope	P^b	Transformation ^c
TOPOGRAPHY AND STRUCTURE				
Distance to intermittent stream (m)	2 (0.2)	114 (13)	0.0001	Log
Distance to permanent stream (m)	2 (0.2)	245 (20)	0.0001	Log
Elevation (m)	288 (15)	421 (21)	0.0001	Log
Slope (%) ^d	47.6 (2.9)	44.6 (3.1)	0.6624	None
Litter depth (mm) ^e	2.1 (0.1)	5.0 (0.2)	0.0001	None
Vegetative cover (%) ^f				
Herb layer	49.1 (2.7)	67.1 (4.7)	0.1351	Logit
Shrubs < 1.3 m	22.3 (1.4)	73.4 (2.7)	0.0016	Logit
Shrubs 1.3-4 m	74.7 (2.1)	24.7 (3.4)	0.0021	Logit
Midstory (4 m to lower canopy)	21.9 (1.6)	11.5 (1.4)	0.0362	Logit
Overstory	43.6 (2.5)	69.6 (1.2)	0.0039	Logit
Basal area (m ² /ha) ^g				
Conifers	17.5 (1.9)	54.5 (3.5)	0.0089	None
Hardwood	8.1 (1.3)	9.2 (2.0)	0.9762	None
Snags	6.0 (0.9)	18.2 (1.6)	0.0146	None
Total	31.7 (2.2)	81.7 (3.7)	0.0034	None
Log lengths (m/ha)				
10-19 cm dia.	233 (31)	227 (31)	0.8170	Log
20-49 cm dia.	354 (40)	348 (44)	0.5735	Log
> 50 cm dia.	865 (111)	414 (42)	0.1834	Log
Total	1452 (134)	990 (61)	0.0953	Log
Stumps ^h /ha	57 (7.2)	150 (13)	0.0188	Log
COMPOSITION (% cover)ⁱ				
Forbs	35.6 (2.4)	10.3 (2.0)	0.0025	Logit
Grasses and sedges	4.2 (0.5)	4.6 (0.8)	0.9650	Logit
Ferns (primarily sword fern)	9.3 (1.3)	52.1 (3.3)	0.0019	Logit
Salal	0.0 (0.0)	17.6 (4.0)	0.0323	Logit
Oregon-grapes	0.0 (0.0)	8.8 (2.0)	0.0149	Logit
Salmonberry	56.4 (3.4)	9.6 (3.2)	0.0030	Logit
Stinking currant	14.4 (2.5)	0.1 (0.1)	0.0400	Logit
Huckleberries	2.1 (0.1)	5.6 (0.7)	0.0124	Logit
Devil's-club	4.0 (1.0)	0.4 (0.4)	0.0002	Logit
Vine maple	17.9 (2.2)	7.0 (1.9)	0.0205	Logit
Elderberries	1.3 (0.6)	0.0 (0.0)	0.0678	Logit
Hazels	1.6 (0.7)	0.0 (0.0)	0.2546	Logit
Plums (<i>Prunus</i> spp.)	0.3 (0.1)	0.0 (0.0)	0.2070	Logit
Ocean-spray (<i>Holodiscus discolor</i>)	0.1 (0.1)	0.3 (0.1)	0.2604	Logit
Rhododendrons (<i>Rhododendron</i> spp.)	0.0 (0.0)	0.6 (0.5)	0.2729	Logit
Red alder	40.4 (3.9)	23.3 (4.0)	0.0842	Logit
Bigleaf maple	3.7 (1.1)	0.1 (0.1)	0.2051	Logit
Douglas-fir	14.4 (2.4)	58.7 (3.5)	0.0047	Logit
Western hemlock	10.5 (1.8)	9.9 (2.7)	0.8267	Logit
Western redcedar	7.1 (1.7)	0.3 (0.2)	0.0392	Logit

^a n = number of transects; each transect had 8 sample points 100 m apart.

^bTwo-way analysis of variance with stand as the block and the stand by transect interaction used as the error term to test transect effects.

^cLog = $\log_{10}$ (value + 1); Logit = $\log$ (proportion of value/(1 - proportion of value)).

^dMeasured with a clinometer 20 m upslope and downslope from plot center.

^eAverage of 9 systematically arranged points 10 m apart/station.

^fOcular estimates of cover.

^gWedge prism tally for basal area.

^hStumps = dead standing stems >10 cm diameter and <2 m tall.

percent correct classification rates to minimize the probability of reporting spurious relationships (Rexstad *et al.* 1988). Interpretation of the results was based on linear correlations between the selected variables and the discriminant scores. For species with < 20 non-capture sites, we used step-wise multiple regression to identify the set of habitat variables that best predicted capture rates/station. Only results with multiple $R^2 > 50$ percent are reported. These analyses should be considered descriptive and exploratory because sample points along transects were distributed among six stands, so points within a stand were likely more dependent on one another than points among stands; hence there is the potential for patterns to be confounded by stand effects. We tried to minimize this effect by analyzing data only for species that occurred in all six stands.

We compared habitat characteristics between streamside and upslope transects with a two-way ANOVA. The stand-by-transect interaction was used to test the transect effect, when appropriate. In instances where residuals were not normally distributed or where variances were heterogeneous, analyses were conducted on transformed (logit, log, or rank) data to more closely meet the assumptions of ANOVA. Where transformations were unsuccessful, a Wilcoxon rank-sum test was used.

Results and Discussion

Habitat Comparisons

In addition to several major physiographic features (elevation and distance to permanent and intermittent streams), nine structural and 12 floristic habitat variables differed between streamside and upslope transects (Table 1). Streamside areas were characterized by having shallower litter depth, greater shrub cover in the 1.3- to 4-m layer, greater midstory cover, less shrub cover in the < 1.3-m layer, less overstory cover, less basal area of snags and live conifers, and fewer stumps than upslope areas. These differences largely result from differences in floristics between streamside and upslope areas. Streamside transects had greater coverage by forbs, salmonberry, vine maple, red alder, stinking currant, elderberries (*Sambucus* spp.), western redcedar, and devil's-club, whereas upslope transects had greater coverage by ferns, salal, Oregon-grapes, huckleberries, and Douglas-fir.

Streamside-Upslope Comparisons and Transriparian Analyses

In 31,200 TN, we caught 2,562 small mammals and 288 amphibians representing 18 of 22 small mammal species and 9 of 13 amphibian species known to occur in the central Oregon Coast Range (Brown 1985: appendix 8).

Small mammals.—Small mammal species diversity was higher on streamside than on upslope transects in the wet season, largely because equitability was higher on streamside than upslope transects (Table 2). Low upslope equitability was caused by the dominance of Trowbridge's shrews and western red-backed voles. The capture rate for all small mammals combined was negatively correlated with the log-linear distance from the stream (Table 3). Community similarity averaged < 55 percent between streamside and upslope transects.

Capture rates of marsh shrews, Pacific jumping mice, long-tailed voles, and white-footed voles were higher along streamside than upslope transects (Table 2). Capture rates of Pacific shrews, marsh shrews, shrew-moles, Pacific jumping mice, and deer mice were inversely related to distance from stream (Table 3) and dropped sharply from 50-100 m from the stream (Figure 1).

Capture rates for western red-backed voles, creeping voles, Trowbridge's shrews, and Townsend's chipmunks were higher along upslope than streamside transects (Table 2). Captures of western red-backed voles were positively associated with distance from the stream (Table 3) and rose abruptly beyond 200 m from the stream (Figure 1).

Neither streamside nor upslope habitats alone seemed to provide adequate habitat for all of the small mammal species that we sampled. These findings differ somewhat from those in the Oregon Cascades and the southern Coast Range. In the western Cascades, small mammal species richness was higher in riparian zones than in habitat 20-30 m upslope from the stream (Anthony *et al.* 1987). In the same area, Doyle (1990) found higher abundance and species richness of small mammals in fourth- and fifth-order streamside zones than in upland forest and higher equitability in upslope than streamside habitats, but these differences were not consistent over years. Five of 10 small mammal species trapped had higher relative abundance in streamside than upland habitat, including species

TABLE 2. Captures/1000 TN of small mammals and amphibians along streamside ($n = 6$) and upslope ($n = 6$) transects in six stands, Lincoln County, Oregon, 1988.

Species	Frequency of occurrence in stands (out of 6)	Captures/1000 TN						P ^a
		Stream			Upslope			
		x	(SE)	(n ^a)	x	(SE)	(n ^a)	
MAMMALS ^c								
Wandering shrew (<i>Sorex vagrans</i>)	4	0.4	(0.2)	(3)	0.4	(0.2)	(3)	0.7842
Pacific shrew	6	11.4	(1.5)	(126)	7.2	(1.1)	(64)	0.1495
Marsh shrew	6	9.4	(1.0)	(105)	0.6	(0.3)	(5)	0.0030
Trowbridge's shrew	6	22.3	(2.0)	(273)	32.8	(2.6)	(372)	0.0247
Shrew-mole	6	2.5	(0.6)	(20)	1.3	(0.4)	(11)	0.2198
Coast mole (<i>S. orarius</i>)	5	1.1	(0.4)	(9)	0.5	(0.2)	(4)	0.3359
Townsend's mole (<i>Scapanus townsendii</i>)	2	0.3	(0.3)	(2)	0.1	(0.1)	(1)	0.9020
Mountain beaver (<i>Aplodontia rufa</i>)	6	0.7	(0.4)	(6)	0.5	(0.2)	(4)	0.4844
Townsend's chipmunk	6	2.5	(0.6)	(6)	11.7	(2.2)	(28)	0.0235
Mazama pocket gopher (<i>Thomomys mazama</i>)	2	0.1	(0.1)	(1)	0.3	(0.2)	(2)	0.5233
Deer mouse	6	10.0	(1.8)	(87)	4.2	(0.9)	(35)	0.2223
Dusky-footed woodrat (<i>Neotoma fuscipes</i>)	1	0.1	(0.1)	(1)	0	(0)	(0)	0.3173
Western red-backed vole	6	1.1	(0.5)	(8)	17.1	(2.9)	(129)	0.0121
White-footed vole	6	1.2	(0.5)	(10)	0.1	(0.1)	(1)	0.0051
Red tree vole (<i>P. longicaudus</i>)	2	0.1	(0.1)	(1)	0.1	(0.1)	(1)	1.0000
Long-tailed vole	4	0.6	(0.3)	(5)	0	(0)	(0)	0.0209
Creeping vole	6	0.5	(0.2)	(4)	2.1	(0.5)	(21)	0.0303
Pacific jumping mouse	6	11.4	(1.8)	(93)	1.3	(0.5)	(12)	0.0076
Total captures		53.0	(3.4)	(765)	48.7	(3.3)	(695)	0.8726
Species richness		7.8	(1.5)		7.4	(1.1)		0.6681
Species diversity (H')		0.70	(0.09)		0.56	(0.07)		0.0211
Equitability		0.80	(0.05)		0.70	(0.06)		0.0062
Community similarity (%)		53.5 (3.5)						
AMPHIBIANS ^c								
Pacific giant salamander	6	1.6	(0.5)	(9)	1.0	(0.4)	(6)	0.4029
Olympic salamander (<i>Rhyacotriton olympicus</i>)	1	0.2	(0.2)	(1)	0	(0)	(0)	0.3173
Roughskin newt (<i>Taricha granulosa</i>)	5	1.7	(0.6)	(10)	1.4	(0.5)	(8)	0.7350
Dunn's salamander	5	1.7	(0.5)	(13)	0.4	(0.2)	(2)	0.0855
Western redback salamander	5	3.0	(0.8)	(21)	2.6	(0.7)	(16)	0.7435
Ensatina salamander	5	0.2	(0.2)	(1)	1.9	(0.6)	(12)	0.0233
Clouded salamander (<i>Aneides ferreus</i>)	2	0.2	(0.2)	(1)	0.2	(0.2)	(1)	1.0000
Tailed frog	6	4.3	(0.8)	(28)	3.2	(0.7)	(22)	0.3289
Red-legged frog (<i>Rana aurora</i>)	1	0	(0)	(0)	0.2	(0.2)	(1)	0.3173
Total captures		10.9	(1.2)	(86)	8.9	(0.9)	(68)	0.2971
Species richness		3.3	(0.8)		3.1	(0.6)		0.4049
Species diversity (H')		0.45	(0.10)		0.39	(0.10)		0.3379
Equitability		0.90	(0.05)		0.89	(0.05)		0.8381
Community similarity (%)		39.6 (5.3)						

^aNumber of captures.

^bWilcoxon rank-sum test.

^cMammal capture rates are based on pitfall and Museum special traps, except Townsend's chipmunks and dusky-footed woodrat rates are based on Museum Specials only and mountain beaver rates are based on pitfalls only. Amphibian capture rates based on pitfall sampling.

found on our study sites: Trowbridge's shrew, deer mouse, Pacific jumping mouse, creeping vole, and ermine (*Mustela erminea*). Doyle (1990) also reported western red-backed voles and Townsend's chipmunks to be more abundant in upslope than riparian habitats. Although most of Doyle's (1990)

findings are similar to ours, deer mice and Trowbridge's shrews seemed to have a stronger affinity for riparian habitat in the central Cascades than in the Coast Range. Cross (1985) reported higher abundances of deer mice, Pacific shrews, shrew-moles, and jumping mice in streamside zones

TABLE 3. Correlations between distance along transriparian transects and capture rates of small mammals and amphibians with ≥ 20 captures* in six mature Douglas-fir stands, Lincoln County, Oregon, 1988 ($n = 54$).

Species	Number of captures	Linear		Log-linear	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
MAMMALS					
Pacific shrew	138	-0.22	0.1116	-0.33	0.0164
Marsh shrew	33	-0.41	0.0019	-0.46	0.0005
Trowbridge's shrew	723	-0.04	0.7543	-0.09	0.5118
Shrew-mole	36	-0.32	0.0180	-0.30	0.0273
Townsend's chipmunk	29	+0.16	0.2566	+0.09	0.5287
Deer mouse	130	-0.53	0.0001	-0.53	0.0001
Western red-backed vole	200	+0.29	0.0340	+0.30	0.0280
Creeping vole	21	+0.18	0.1833	+0.20	0.1444
Pacific jumping mouse	52	-0.57	0.0001	-0.63	0.0001
Total mammals	1414	-0.29	0.0354	-0.33	0.0159
AMPHIBIANS					
Pacific giant salamander	23	-0.10	0.4808	-0.13	0.3590
Western redback salamander	39	+0.06	0.6636	+0.05	0.7000
Ensatina salamander	20	+0.07	0.5921	+0.10	0.4852
Tailed frog	63	-0.21	0.1186	-0.22	0.1100
Total amphibians	177	-0.20	0.1437	-0.24	0.0826

*Other species captured along the transriparian transects include: clouded salamander (1), wandering shrew (8), coast mole (13), Townsend's mole (1), mountain beaver (13), Mazama pocket gopher (2), white-footed vole (5), red tree vole (3), ermine (1), rough-skin newt (12), Dunn's salamander (9), red-legged frog (1), and Olympic salamander (1).

than in upland or transition zones in southwest Oregon.

Amphibians.—Amphibian species richness, equitability and diversity did not differ between streamside and upslope transects, even though community similarity was < 40 percent between the 2 habitat types (Table 2). Total amphibian captures declined with increasing distance from the stream along the transriparian transect, but this relationship was weak ($r = 0.24$, $P = 0.08$, Table 3). Although some amphibian species require streams or ponds for reproduction, total amphibian captures were not associated with streamside habitat (Table 3).

More Dunn's salamanders were caught along streamside than upslope transects, whereas more ensatinas were caught along upslope than streamside transects (Table 2). No amphibian species exhibited associations with distance from stream along the transriparian transects ($r < 0.22$).

Habitat Associations

Discriminant functions with correct classification rates > 80 percent were obtained for only three of 10 species with ≥ 20 capture sites and ≥ 20 non-capture sites. In all three models, distance to

either intermittent or permanent streams was useful for discriminating capture sites from non-capture sites. Correct classification rates were < 80 percent for deer mice (74%), Townsend's chipmunk (70%), shrew-mole (55%), Pacific shrew (70%), tailed frog (59%), western redback salamander (*Plethodon vehiculum*) (75%), and Pacific giant salamander (*Dicamptodon tenebrosus*, 67%). A multiple regression model to predict Trowbridge's shrew captures at each trap station was also weak ($R^2 = 16\%$).

Western red-backed vole.—Capture sites were distinguished from non-capture sites by having less alder and forb coverage, greater coverage by Oregon-grapes and ferns, and by being farther from a stream (canonical $R^2 = 45\%$, Table 4). Upslope areas dominated by Douglas-fir and associated shrub and fern communities characterized habitat for western red-backed voles, consistent with the description of habitat given by Maser *et al.* (1981:196).

Pacific jumping mouse.—Capture sites were distinguished from non-capture sites by being closer to a permanent stream and having less coverage of shrubs < 1.3 m tall (canonical $R^2 = 49\%$, Table 4). Early seral stage patches within the streamside

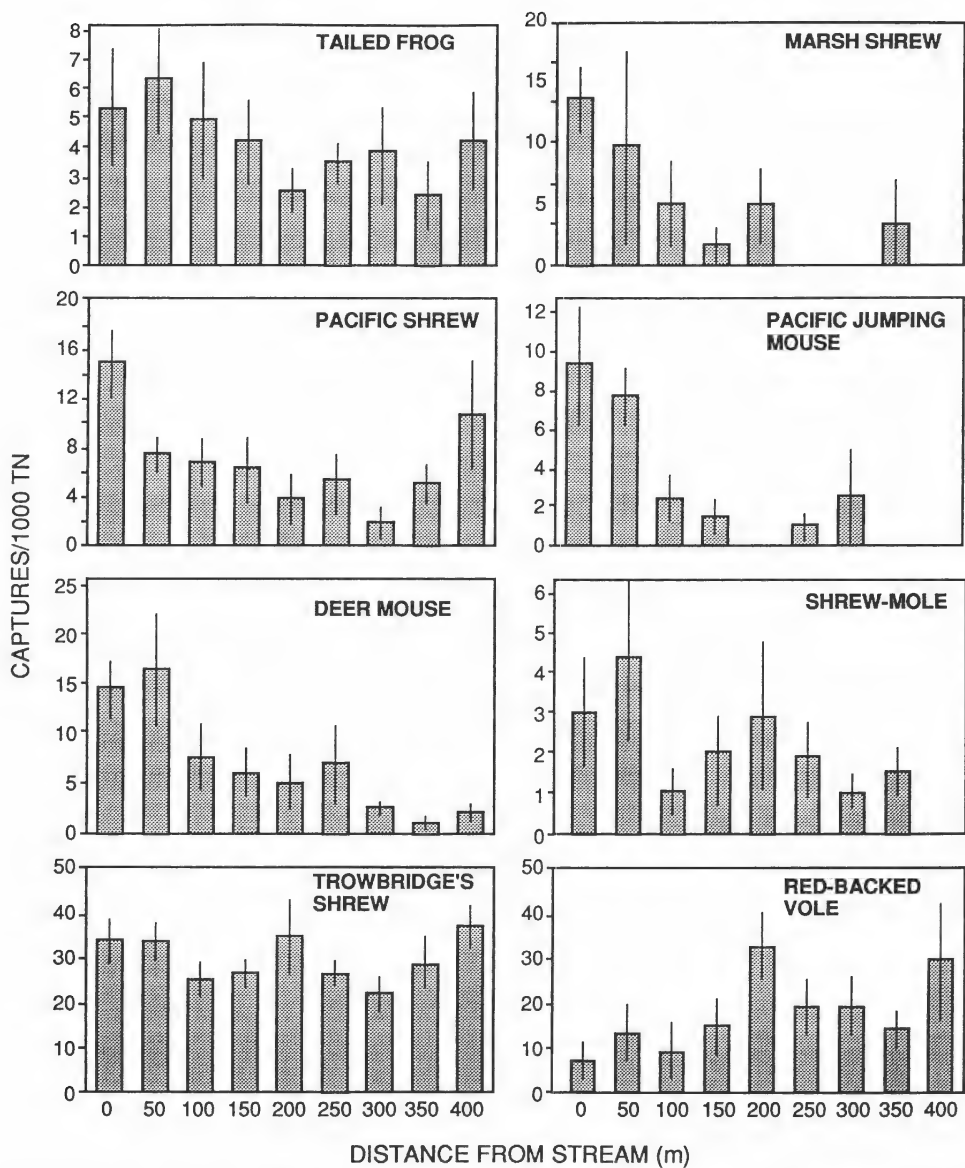


Figure 1. Average captures/1000 TN of 8 species along trans riparian transects in six unmanaged, mature forest stands, Lincoln County, Oregon, 1988. Vertical bars indicate standard errors.

TABLE 4. Variables included in discriminant models for small mammals species in 6 mature Douglas-fir stands, Lincoln County, Oregon, 1988. Only correlation coefficients ≥ 0.25 with DFA scores are presented.

Species	n ^a	Habitat Feature	r with DFA
California red-backed vole	94/86	Alder cover	-0.76
		Oregon-grape cover	+0.65
		Dist. to intermittent stream	+0.63
		Forb cover	-0.61
		Fern cover	+0.56
Pacific jumping mouse	63/117	Dist. to permanent stream	-0.67
		Shrub cover < 1.3 m tall	-0.58
		Stump density	-0.48
		Alder cover	+0.47
		Elevation	-0.46
		Hazel cover	+0.29
Marsh shrew	54/126	Dist. to permanent stream	-0.95
		Forb cover	+0.67
		Hazel cover	+0.39

^an = Number of capture sites/number of non-capture sites.

area characterized jumping mouse habitat in our stands, consistent with the description provided by Maser *et al.* (1981:232).

Marsh shrew.—Capture sites were distinguished from non-capture sites by being closer to a permanent stream and having greater coverage by forbs and hazel (canonical $R^2 = 43\%$, Table 4). They feed on aquatic insects and terrestrial invertebrates at the water's edge (Whitaker and Maser 1976), but little is known about the habitat needs of this species.

Management Implications

Both streamside (24 species) and upslope (23 species) habitats contributed to the total species richness of 25. Some species occurred in lower numbers in one of these two habitats compared to the other, so small mammal and amphibian community structures differed between these streamside and upslope habitats.

Guidelines contained in the Oregon Forest Practices Act state that a riparian management area (RMA) with an average of three times the stream width (but not less than 7.6 m and not more than 30.3 m wide) shall be maintained on all fish-bearing streams. Within RMA's all logs on the ground prior to harvest, some live conifers, 50 percent of the preharvest shade level, and 75 percent of the shade over the aquatic zone must be retained following harvest. Federal land management agencies sometimes leave wider (30-50 m) RMA's to meet other needs, such as snag requirements. Tim-

ber harvest, which is usually in the form of clear-cutting, may occur outside of RMA's. If RMA's are > 50 m on each side of the stream and managed to provide mature forest habitat for small mammals and amphibians, then most of the species that we sampled might find at least marginal habitat in RMA's prior to harvest of adjacent upslope areas. Marsh shrews, Pacific jumping mice, long-tailed voles, and white-footed voles might find optimal habitat in streamside areas. Harvesting adjacent upslope areas will have unknown effects on habitat quality within RMA's for the species that we sampled. For instance, if any of these species are adversely affected by induced edges (Brown 1985:119, *sensu* Temple 1986), then narrow RMA's may not even provide marginal habitat for such species.

Harris (1984:146-147) suggested that riparian areas could be used to link mature forest stands within landscapes. If streamside areas are intended to function as corridors, then consideration should be given to corridor width. Because of the dynamic nature of streamside systems [fluvial events and beaver (*Castor canadensis*) activity], they tend to be structurally and compositionally more complex than upslope areas. Narrow corridors (< 50 m) with patchily distributed mature forest may not be sufficient as dispersal corridors for species strongly associated with one seral stage. Further study is needed to determine the level of forest disturbance that could occur in RMA's and still maintain optimal habitat for small mammals and amphibians.

Our data indicate that streamside corridors in mature forests may not be sufficient linkages for western red-backed voles. If land managers wish to promote linkages among upslope mature forest patches, then streamside corridors should be sufficiently wide to include optimal habitat used by western red-backed voles until additional data can be collected within streamside buffer strips to assess their value. Alternatively, intervening managed forest stands could be made more permeable to this species by retaining significant amounts of within-stand structure during harvest (green trees, snags, and logs), or by providing upslope corridors.

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Literature Cited

- Anthony, R. G., E. D. Forsman, G. A. Green, G. Witmer, and S. K. Nelson. 1987. Small mammal populations in riparian zones of different aged coniferous forests. *Murrelet* 68:94-102.
- Brazier, J. R., and G. W. Brown. 1973. Buffer strips for stream temperature control. *For. Res. Lab., Oreg. State Univ. Res. Pap.* 15. 9 pp.
- Brower, J. E., and J. H. Zar. 1984. Field and laboratory methods for general ecology. W. C. Brown Publ., Dubuque, Iowa. 226 pp.
- Brown, E. R., ed. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. U.S. Dep. Agric. For. Serv. Publ. No. R6-F & WL-192-1985. 332 pp.
- Cross, S. P. 1985. Responses of small mammals to forest riparian perturbations. *In* Proc. Conf. on Riparian ecosystems and their management. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-120.
- Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. *J. Mammal.* 71:14-23.
- Geier, A. R., and L. B. Best. 1980. Habitat selection by small mammals of riparian communities: evaluating effects of habitat alterations. *J. Wildl. Manage.* 44:16-24.
- Harris, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. Univ. Chicago Press, Chicago. 211 pp.
- Johnson, R. R., and C. H. Lowe. 1985. On the development of riparian ecology, pages 112-116 *in* Proc. Sympos. Riparian ecosystems and their management. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-120.
- Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981. Natural history of Oregon Coast mammals. U.S. Dep. Agric. For. Serv. Tech. Rep. PNW-133. 496 pp.
- McComb, W. C., R. G. Anthony, and K. McGarigal. 1991. Differential vulnerability of small mammals to two trap types and two trap baits. *Northw. Sci.* 65:109-115.
- Rexstad, E. A., D. D. Miller, C. H. Flather, E. M. Anderson, J. W. Hupp, and D. R. Anderson. 1988. Questionable multivariate statistical inference in wildlife habitat and community studies. *J. Wildl. Manage.* 52:794-798.
- Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: comparison of two models. *In* J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates*. Univ. of Wisconsin Press, Madison. Pp. 301-304.
- Whitaker, J. O., Jr., and C. Maser. 1976. Food habits of five western Oregon shrews. *Northw. Sci.* 50:102-107.
- Williams, B. K., K. Titus, and J. E. Hines. 1990. Stability and bias of classification rates in biological applications of discriminant analysis. *J. Wildl. Manage.* 54:331-341.

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Fishes of the Lower Willamette River, Near Portland, Oregon

Abstract

We used a variety of gears to collect information on fish species present in the lower Willamette River as part of a study to evaluate the effects of harbor developments on anadromous and resident fish. We identified 39 fish species from 17 families. Nineteen species from seven families were exotic to the Willamette River system. When possible, we described distribution and relative abundance of individual species. Information about fish species present in the lower Willamette River will help fisheries managers assess potential effects of future development options on fish populations based on habitat requirements of fish species present.

Introduction

The Willamette River near Portland, Oregon supports a recreational fishery for anadromous fish including chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, steelhead *O. mykiss*, American shad *Alosa sapidissima*, and white sturgeon *Acipenser transmontanus* in a major metropolitan area. Resident species such as largemouth bass *Micropterus salmoides*, black crappie *Pomoxis nigromaculatus*, white crappie *P. annularis*, and walleye *Stizostedion vitreum vitreum* also support fisheries. Many other resident species are also present, including northern squawfish *Ptychocheilus oregonensis*, a major predator of juvenile salmonids (Thompson 1959, Beamesderfer and Rieman 1991).

Few studies have been conducted to determine the status and population structure of resident fish species in the Willamette River. Dimick and Merryfield (1945) described relationships between fish species distribution and pollution in the Willamette River, but did not sample downstream from river kilometer (Rkm) 27. Hjort *et al.* (1984) studied fish assemblages at revetments in the middle and upper mainstem Willamette River. Hughes and Gammon (1987) evaluated effects of improved water quality of the Willamette River on fish assemblages, but they conducted only limited sampling in the harbor area.

Habitat in the Willamette River near Portland has been altered to accommodate urban development and a growing shipping industry. Knowledge of fish populations in the area may enable fishery managers to predict better the effects proposed habitat alterations would have on fish populations. Our objective is to list species found in the lower Willamette River and describe their distribution and relative abundance. Data were collected as

part of a cooperative study by the Oregon Department of Fish and Wildlife (ODFW) and the Port of Portland to evaluate the effects of waterway development on fish populations in the lower Willamette River (Ward *et al.* 1991, Ward 1992).

Study Area

Fish were collected in the Willamette River from its confluence with the Columbia River upstream to river kilometer (Rkm) 27 (Figure 1). Most sampling was conducted downstream from Rkm 19. Most development is within Portland Harbor and lies between Rkm 5 and Rkm 17. Artificial structures (piers, wharfs, etc.) in Portland Harbor have changed the natural shoreline to riprap, bulkheads and sand-beached lagoons. Because of dredging, the river has a steeply sloped, silt and sand bottom. Water depths average 12-14 m with a maximum depth of 24 m. Except when affected by structure, water velocity was similar throughout the harbor, even during spring when flows were high. River flow from 1987 to 1989 averaged between 24,190 and 29,080 cfs with a high over 170,000 cfs during January 1988 and a low of 6,980 cfs during August 1988.

Predominant geographical features in the study area include Multnomah Channel (Rkm 5), an important waterway for migrating spring chinook salmon; Swan Island (Rkm 12), a heavily developed industrial peninsula and backwater that supports a popular warmwater fishery; and Ross Island (Rkm 24), which separates the main channel from Willamette Slough (Figure 1).

Methods

We sampled nine sites in the lower Willamette River from March through June and in November

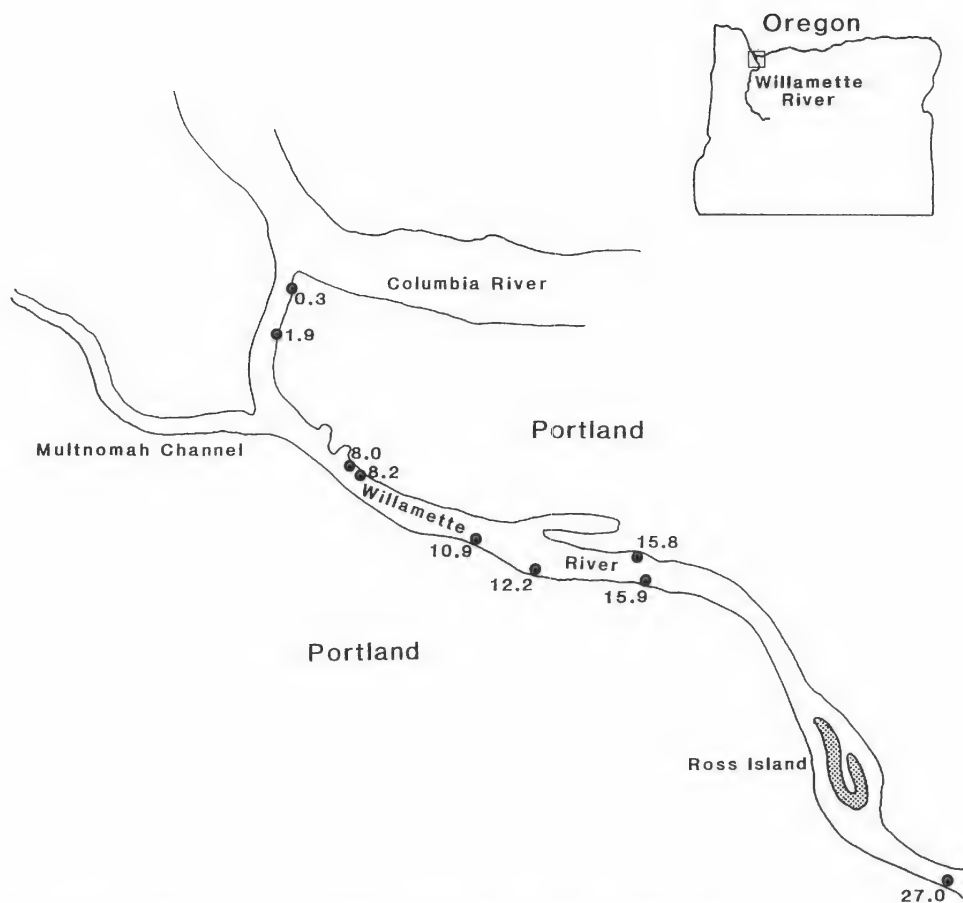


Figure 1. Locations of sampling (designated by Rkm) in the Lower Willamette River, Oregon.

from 1987 through 1990 (Figure 1). Five sampling sites were selected because they contained unique structures (Table 1). Four additional sites were selected because they contained no structure. Sampling periods coincided with times of expected migration of juvenile salmonids. We used six gear types to capture fish: bottom and vertical gillnets, an electrofishing boat, trap nets, beach seines, and purse seines. Bottom gillnets measured 45.6-m long by 2.4-m deep. Each half consisted of three 7.6-m long monofilament nylon panels of 3.2-cm, 4.4-cm, and 5.1-cm bar mesh. We set nets parallel or perpendicular to shore, and adjacent to or within structures if present. Nets were fished for one hour. Vertical gillnets were 3-m long by 18-m

TABLE 1. Description of sampling areas in the lower Willamette River.

Sampling area (river kilometer)	Structure, support	Shoreline
0.3	None	Sandy beach
1.9	Offshore wharf, pilings	Sandy beach
8.0	Wharf, backfill	Vertical wall
8.2	Floating platform	Riprap, sandy beach
10.9	None	Riprap, sandy beach
12.2	Pier, pilings	Clay beach
15.8	None	Riprap, sandy beach
15.9	Wharf, pilings	Riprap
27.0	None	Sandy beach

deep, with either 0.20-cm or 0.30-cm bar mesh nylon monofilament. Nets were fished through the water column at various distances from shore for one hour. The electrofishing boat was equipped with a 5,000-watt alternator and a variable voltage pulsator unit that provided an output capacity of 0 to 1,000 volts DC. We electrofished parallel to shore and along structures. The voltage and pulse-width were varied so that current ranged from 4 to 6 amperes. Power was pulsed on and off so that each 15-minute power-on shocking run was completed in approximately 22-23 minutes. The trap net was 1.8-m deep with a 30-m long lead with 0.20-cm bar mesh. The net was set perpendicular to shore with the lead in water less than 1.8-m deep. The trap net was fished for 24 hours and then pulled and re-set at another site. The beach seine was 22.9-m long and 1.8-m deep with 0.10-cm bar mesh knotless nylon netting. Attached were two 15.2-m long wings with 0.20-cm bar mesh knotless nylon netting. The beach seine was deployed on clear beaches. The purse seine was 61-m long and 6.1-m deep with 0.20-cm bar mesh knotless nylon netting, except for the 22.9-m long bunt end with 0.10-cm bar mesh knotless nylon netting. Beach seine and purse seine hauls took about 10 minutes. Gillnetting and electrofishing were conducted after sunset. Beach and purse seining were conducted mostly during daylight. Catches were identified to species and counted.

Catches from all gears were used to develop a list of species present in the lower Willamette River. We summed bottom gillnet and electrofishing catch and effort for each sampling site. Differences in catch, if any, among sampling sites were noted. Because most of our effort took place from March through June, only catch and effort during these months were included in our summary. Because trap-net effort was limited to eight, 24-hr sets during spring, 1990, we did not compare catches in the trap net among sites. Because catches in seines and vertical gillnets consisted almost entirely of migrating juvenile salmonids, these gears were also not included in comparisons of catch among sampling sites.

Results and Discussion

Thirty-nine fish species from 17 families were collected in the lower Willamette River (Table 2). We collected or observed 37 species, and anglers collected two additional species (pirapatinga *Piaractus*

TABLE 2. Thirty-nine species of fish from 17 families collected in the lower Willamette River, 1987-1990. Asterisk denotes introduced species.

Family, species	Common Name
Petromyzontidae	
<i>Lampetra tridentata</i>	Pacific lamprey
Acipenseridae	
<i>Acipenser transmontanus</i>	white sturgeon
Clupeidae	
<i>Alosa sapidissima</i>	*American shad
Salmonidae	
<i>Oncorhynchus kisutch</i>	coho salmon
<i>Oncorhynchus tshawytscha</i>	chinook salmon
<i>Oncorhynchus mykiss</i>	steelhead (rainbow trout)
<i>Oncorhynchus nerka</i>	*sockeye salmon
<i>Oncorhynchus clarki</i>	cutthroat trout
<i>Prosopium williamsoni</i>	mountain whitefish
Osmeridae	
<i>Thaleichthys pacificus</i>	eulachon
Cyprinidae	
<i>Ptychocheilus oregonensis</i>	northern squawfish
<i>Mylocheilus caurinus</i>	peamouth
<i>Acrocheilus alutaceus</i>	chiselmouth
<i>Cyprinus carpio</i>	*common carp
<i>Carassius auratus</i>	*goldfish
<i>Richardsonius balteatus</i>	redside shiner
<i>Rhinichthys cataractae</i>	longnose dace
Catostomidae	
<i>Catostomus macrocheilus</i>	largescale sucker
<i>Catostomus platyrhynchus</i>	mountain sucker
Ictaluridae	
<i>Amerius natalis</i>	*yellow bullhead
<i>Amerius nebulosus</i>	*brown bullhead
<i>Ictalurus punctatus</i>	*channel catfish
Gasterosteidae	
<i>Gasterosteus aculeatus</i>	threespine stickleback
Percopsidae	
<i>Percopsis transmontana</i>	sand roller
Percichthyidae	
<i>Morone hybrid</i>	*hybrid bass (white bass <i>M. chrysops</i> X striped bass <i>M. saxatilis</i>)
Cyprinodontidae	
<i>Fundulus diaphanus</i>	*banded killifish
Centrarchidae	
<i>Pomoxis annularis</i>	*white crappie
<i>Pomoxis nigromaculatus</i>	*black crappie
<i>Micropterus dolomieu</i>	*smallmouth bass
<i>Micropterus salmoides</i>	*largemouth bass
<i>Lepomis macrochirus</i>	*bluegill
<i>Lepomis gibbosus</i>	*pumpkinseed
<i>Lepomis gulosus</i>	*warmouth
Percidae	
<i>Stizostedion vitreum vitreum</i>	*walleye
<i>Perca flavescens</i>	*yellow perch
Cottidae	
<i>Cottus asper</i>	prickly sculpin
<i>Cottus perplexus</i>	reticulate sculpin
Characidae	
<i>Piaractus brachyomus</i>	*pirapatinga
Pleuronectidae	
<i>Platichthys stellatus</i>	starry flounder

TABLE 3. Catch in bottom gillnets at nine sites in the Lower Willamette River, March-June, 1987-1990; number of 1-hr sets at each site is given in parentheses. Carp were common, but not counted.

Species	Sampling sites (river kilometer)								
	0.3	1.9	8.0	8.2	10.9	12.2	15.8	15.9	27.0
	(75)	(139)	(140)	(137)	(75)	(137)	(75)	(137)	(132)
White sturgeon	157	23	150	74	14	111	105	9	15
American shad	9	7	7	5	5	9	9	8	14
Chinook salmon ^a	9	8	7	4	9	2	10	1	15
Steelhead ^a	13	28	18	16	35	33	54	54	66
Northern squawfish ^b	114	75	45	35	54	60	49	26	105
Peamouth	298	127	144	123	47	80	150	170	174
Largescale sucker	369	363	143	145	209	201	193	295	250
Yellow bullhead	0	1	5	1	1	3	1	7	0
Brown bullhead	1	2	9	0	1	3	3	8	4
White crappie	0	0	9	2	1	3	1	16	2
Black crappie	2	12	26	16	3	11	2	19	3
Bluegill	0	0	1	0	2	2	0	1	1
Pumpkinseed	0	0	0	0	0	0	0	0	2
Walleye	5	5	3	4	9	5	3	0	2
Yellow perch	3	3	4	2	2	4	2	3	3
Starry flounder ^c	4	0	1	0	0	0	1	0	4

^aAdult fish only.

^bFish ≥ 200 mm.

^cJuvenile fish only.

brachyomus and hybrid bass *Morone* hybrid). Because of size and species selectivity of the gears we used, information is limited for some species and may not represent the true abundance and diversity of all fishes present in the study area.

Acipenseridae

We caught white sturgeon in our bottom gillnets throughout the study area (Table 3). Catch rates were highest at Rkm 0.3 and Rkm 15.8, two sites characterized by a sandy beach shoreline with no structures present.

Salmonidae

Adult and juvenile anadromous salmonids are common in the Willamette River during various times of the year. There also appears to be some overwintering of juvenile chinook salmon in the lower river (Knutsen and Ward 1991). We collected very few coastal cutthroat trout, resident rainbow trout, or mountain whitefish.

Cyprinidae

Northern squawfish were common throughout the study area, especially at sites with no structure present (Tables 3 and 4). Peamouth and carp were also abundant and distributed throughout the study

area (Table 3). As with other populations in the northwest (Wydoski and Whitney 1979), the brilliant red spawning colors of peamouth were most evident during May. The catch of carp increased as water temperatures rose through the spring sampling season.

Less abundant cyprinids included chiselmouth, goldfish, redbreasted shiner, and longnose dace. Redbreasted shiner were rare but caught at all sampling sites. We identified only one longnose dace.

Catostomidae

Largescale suckers dominated our catch of catostomids, and comprised 40% of our total bottom-gillnet catch (Table 3). Largescale suckers were distributed throughout the study area. We collected very few mountain suckers, and most were juveniles.

Centrarchidae

Black crappie, white crappie, and largemouth bass were the most abundant centrarchids in the lower Willamette River (Tables 3 and 4). All three species were most abundant at Rkm 15.9, an area characterized by a wharf with closely-spaced pilings, a completely riprapped shoreline, and a shallow backwater area immediately downstream from the wharf.

TABLE 4. Electrofishing catch at nine sites in the Lower Willamette River, March-June 1987-1990; number of 15-min shocking runs at each site is given in parentheses. All northern squawfish (≥ 200 mm fork length), centrarchids, walleye, and yellow perch (≥ 200 mm fork length) were counted. Many other species were encountered but not always counted.

Species	Sampling sites (river kilometer)								
	0.3	1.9	8.0	8.2	10.9	12.2	15.8	15.9	27.0
Northern squawfish ^a	(42)	(45)	(42)	(43)	(43)	(43)	(43)	(43)	(43)
White crappie	14	33	24	22	18	15	25	14	17
Black crappie	0	2	5	0	12	4	2	69	1
Bluegill	12	5	3	1	19	4	4	133	4
Pumpkinseed	2	0	2	0	3	2	0	49	2
Smallmouth bass	0	1	1	0	2	0	0	16	0
Largemouth bass	1	0	5	1	13	12	5	40	13
Walleye	2	1	2	0	14	5	2	115	2
Yellow perch ^a	2	5	0	0	14	3	0	0	1
	3	7	2	5	7	8	7	22	11

^aFish ≥ 200 mm; many fish < 200 mm were encountered but not counted.

Other centrarchids collected included smallmouth bass, bluegill, pumpkinseed, and warmouth. We caught most smallmouth bass and bluegill at RKm 15.9 (Table 4). Pumpkinseed and warmouth were relatively rare.

Percidae

Although relatively uncommon, we caught walleye throughout the study area (Tables 3 and 4). Catch was highest at RKm 10.9. Yellow perch were abundant and evenly distributed throughout the study area, but we caught few yellow perch ≥ 200 mm fork length (Table 4).

Others

Fish species we observed but collected little information from included Pacific lamprey (Petromyzontidae), American shad (Clupeidae), eulachon (Osmeridae), yellow and brown bullheads and channel catfish (Ictaluridae), three-spine stickleback (Gasterosteidae), sand roller (Percopsidae), banded killifish (Cyprinodontidae), prickly and reticulate sculpin (Cottidae), and starry flounder (Pleuronectidae). We caught one eulachon (smelt) in a gillnet. Ictalurid catches were low and we caught only one channel catfish. We collected a few banded killifish at RKm 27.0. Sculpin were common throughout the study area. Prickly sculpin comprised about 85% of the sculpins we identified to species. Starry flounder juveniles were occasionally caught throughout the study area, primarily at sites with no development.

Three striped bass x white bass hybrids (Percichthyidae) and two pirapatinga (Characidae) were

caught by anglers. The hybrid bass were collected at RKm 10.9. These fish may have been migrants from an experimental program in southwestern Oregon, or may have been illegally introduced. The pirapatinga were caught at RKm's 6.4 and 17.7. It was not determined if these fish were from an illegal introduction or were part of a hoax; however, one specimen appeared to have been in the river for at least a short period of time based on stomach contents (Jay Massey, Oregon Department of Fish and Wildlife, personal communication).

Summary and Conclusions

The diversity of our catch (39 species from 17 families) was greater than that of previous studies in the Willamette River. Dimick and Merryfield (1945) collected 34 species from 13 families in the Willamette River, but collected only four species from three families near Portland. The high level of industrial and domestic sewage, and extremely low levels of dissolved oxygen in the lower Willamette River during the 1940's reduced the survival of most fish species. Hughes and Gammon (1987) collected only 28 species from nine families. Hjort *et al.* (1984) collected 28 species from eight families. The increased diversity of our catch probably resulted from increased water quality since the 1940's, our wide variety of sampling gears, and our extended study period.

Three fish species in addition to those we observed have been reported present in the lower Willamette River (Bond 1973, and Wydoski and Whitney 1979). These include Pacific brook lamprey *Lampetra pacifica*, speckled dace *Rhinichthys*

osculus, and tench *Tinca tinca*. Several species of sculpin are found in the Willamette and Lower Columbia rivers, but only a few are likely to be found near Portland. The number of sculpin (20) and dace (1) we identified to species was limited; therefore, speckled dace and other sculpin species may have been present in our catch.

Of the 39 species we observed, 19 species from seven families were exotic to the Willamette River system (Table 2). The first carp introduction into the area was made in the early 1880's as a food fish (Wydoski and Whitney 1979). All centrarchids were established in the Willamette River at or near Portland during and shortly after the Lewis and Clark Exposition held in Portland in 1905 (Dimick and Merryfield 1945). The ictalurids were introduced in the late 1800's and early 1900's (Wydoski and Whitney 1979). American shad were introduced in 1886 (Dimick and Merryfield 1945). Sockeye salmon were introduced into up-river reservoirs that resulted in adult returns starting in 1970 (Bennett and Foster 1990). This run is being eliminated by ODFW by removing returning adults. Banded killifish were illegally introduced into the Willamette River system in the late 1970's or early 1980's (Dr. D. Markle, Oregon State University, personal communication). The hybrid bass and pirapatinga were found in the Willamette River in 1989.

Walleye were not found in the Willamette River as recently as 1979 (Li *et al.* 1979). The first recorded catch of walleye in the Willamette River was in March 1981 (Don Bennett, Oregon Department of Fish and Wildlife, personal communication). Since their introduction into the Columbia River system near Lake Roosevelt in the 1940's or 1950's (Beamesderfer and Nigro 1989), walleye have gradually spread downriver, and have now established an apparently limited population in the Willamette River.

Literature Cited

- Anonymous. 1988. Willamette basin fish management plan. Oregon Department of Fish and Wildlife, Portland.
- Beamesderfer, R. C., and A. A. Nigro. 1989. Status, biology and alternatives for management of walleye in John Day Reservoir: a review. Oregon Department of Fish and Wildlife, Informational Report (Fish) #89-2, Portland.
- Beamesderfer, R. C., and B. E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:439-447.

It is apparent that the relative abundance of various fish species differs among sites we sampled in the lower Willamette River. White sturgeon, important to both sport and commercial fisheries in the Columbia River system, were most abundant at two undeveloped sites. We do not know if white sturgeon were actively avoiding areas that had undergone significant habitat alterations, but our results indicate the possibility of adverse effects of development on white sturgeon populations.

Northern squawfish were also more abundant at undeveloped than developed sites. Because northern squawfish are the primary predator of juvenile salmonids in the Columbia River system (Beamesderfer and Rieman 1991), effects of development on the distribution of northern squawfish is important to fishery managers.

Centrarchids were most abundant at Rkm 15.9, a site characterized by the presence of a backwater and riprapped shoreline. It would seem that similar development in other areas might enhance crappie and bass populations; however, management of these species is dependent upon effects on salmonids (Anonymous 1988). The lower Willamette River offers fishery managers the opportunity to provide a diverse fishery in a major metropolitan area. Careful management decisions concerning development will ensure healthy fish populations and a productive fishery.

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- Bennett, D. E., and C. A. Foster. 1990. 1989 Willamette River spring Chinook salmon run, fisheries, and passage at Willamette Falls. Annual Report. Oregon Department of Fish and Wildlife.
- Bond, C. E. 1973. Key to Oregon freshwater fishes. Technical Bulletin 58. Agriculture Experiment Station. Oregon State University, Corvallis, Oregon.
- Dimick, R. E., and F. Merryfield. 1945. The fishes of the Willamette River system in relation to pollution. Oregon Engineering Experimental Station Bulletin Number 20.

- Hjort, R. C., P. L. Hulett, L. D. LaBolle, and H. W. Li. 1984. Fish and invertebrates of revetments and other habitats in the Willamette River, Oregon. Technical Report E-84-9. Oregon State University for U.S. Army Engineer Waterway Experiment Station, Vicksburg, Mississippi.
- Hughes, R. M., and J. R. Gammon. 1987. Longitudinal changes in fish assemblages and water quality in the Willamette River, Oregon. *Trans. Amer. Fish. Soc.* 116:196-209.
- Knutsen, C. J., and D. L. Ward. 1991. Behavior of juvenile salmonids migrating through the Willamette River near Portland. Oregon Department of Fish and Wildlife. Informational Report (Fish) #91-5, Portland.
- Li, H. W., C. B. Schreck, R. A. Tubbs, and H. F. Horton. 1979. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. First Quarterly Report. Oregon Cooperative Fisheries Research Unit and Oregon Department of Fish and Wildlife.
- Thompson, R. B. 1959. Food of the squawfish of the lower Columbia River. U.S. Fish and Wildlife Service. Fisheries Bulletin Number 158.
- Ward, D. L. 1992. Effects of waterway development on anadromous and resident fish in Portland Harbor. D. L. Ward (ed.) Oregon Department of Fish and Wildlife, Fish Research Project (unnumbered), Final Report, Portland.
- Ward, D. L., C. J. Knutsen, and R. A. Farr. 1991. Status and biology of black crappie and white crappie in the lower Willamette River near Portland, Oregon. Oregon Department of Fish and Wildlife Informational Report (Fish) #91-3, Portland.
- Wydoski, R. S., and R. R. Whitney. 1979. Inland fishes of Washington. University of Washington Press, Seattle.

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Greg L. Schroer,¹ Olympic National Park, 600 E. Park Avenue, Port Angeles, Washington 98362

Kurt J. Jenkins,² National Park Service Cooperative Park Studies Unit, College of Forestry, Oregon State University, Corvallis, Oregon 97331

Bruce B. Moorhead, Olympic National Park, 600 E. Park Avenue, Port Angeles, Washington 98362

Roosevelt Elk Selection of Temperate Rain Forest Seral Stages in Western Washington

Abstract

We studied habitat selection by Roosevelt elk (*Cervus elaphus roosevelti*) in a temperate rain forest in the lower Queets River Valley of the western Olympic Peninsula, Washington from June 1986-June 1987. Elk annual home ranges included predominantly unlogged forests protected within Olympic National Park and logged, regenerating forests adjacent to the park. Radio-collared elk selected valley floors during all seasons except winter, when elk frequently used an adjoining plateau 60 m above the floodplain. In winter, radio-collared elk selected 6-15 year-old clearcuts, which were available on the plateau. Elk selected mature deciduous forests of the valley floor during spring, summer, and autumn, and generally they selected old-age Sitka spruce forests during autumn and winter. Young clearcuts (1-5 years old) and even-aged, regenerating stands (16-150 years old) generally were avoided during all seasons. Management practices that retain preferred habitats of elk, such as deciduous forests, 6-15 yr-old coniferous stands, and old-age coniferous bottomland forests will benefit elk, particularly on elk ranges managed for short-rotation, even-aged stands. Silvicultural alternatives to typical even-aged stand management, such as uneven-aged management and commercial thinning, should also be considered for improving and maintaining interspersed of forage and cover.

Introduction

Logging has altered habitats of Roosevelt elk *Cervus elaphus roosevelti* throughout the Pacific Northwest. Since the turn of the century, most low-elevation old-age forests (>150 years) within the range of Roosevelt elk in Oregon and Washington have been cut for wood products and converted to even-aged stands harvested in 60-90 year cutting cycles (Juday 1977, Meslow *et al.* 1981). For example, low elevation Douglas-fir (*Pseudotsuga menziesii*) forests greater than 200 years old cover about 10 percent of their original distribution (Franklin *et al.* 1981, Franklin and Spies 1984).

Extensive conversion of old-age forests to even-aged stands in short-term harvest rotations may have significant long-term effects on elk populations. These effects include reduced availability of preferred elk habitats and forage (Harris *et al.* 1982, Witmer and deCalesta 1983, Schroer *et al.* 1988); reduced plant species richness and diversity, particularly in pole-sized stands (Franklin and Pechanec 1968, Alaback 1982); and increased disturbance caused by roads (Witmer and deCalesta 1985, Schroer 1987). Greater understanding of elk habitat preferences relative to

forest successional stages would be useful for long range planning of forest harvesting in the Pacific Northwest.

Previous studies of habitat use indicated that old-age coniferous forests, deciduous forests, and some young age-classes of logged coniferous forests are important habitats for Roosevelt elk (Witmer and deCalesta 1983, Jenkins and Starkey 1984, Schroer 1987, Brunt *et al.* 1989). Those studies, however, did not include a broad array of successional ages of forest which permit an assessment of all stages of forest succession. The purpose of this study, therefore, was to determine habitat use patterns of Roosevelt elk whose home ranges included unlogged forests protected within Olympic National Park (ONP) and a variety of successional forests resulting from logging adjoining the park.

Study Area

The study was conducted along 15 km of the lower Queets River Valley in and adjacent to the Queets Corridor of Olympic National Park. The corridor is a strip of national park land (1-3 km-wide) that extends along both sides of the Queets River for approximately 20 km, from the interior core of ONP west to the Quinault Indian Reservation. The Queets corridor was added to ONP in 1945 to protect riparian communities and adjoining areas on the broad floor of Queets River Valley.

¹Present address: Resources Northwest, Inc., 1800 112th Avenue NE, Ste 100, Bellevue, WA 98004.

²Present address: Wrangell-St. Elias National Park and Preserve, P.O. Box 29, Glennallen, AK 99588

The principal landform in the study area is a broad, glacial outwash plain that is predominant along the southwestern edge of the Olympic Mountain Range (Tabor 1975). The Queets River has cut into this plain and created a 1-2.5 km wide valley floor. The valley floor is about 60 m in elevation with at least 4 levels of alluvial terraces (Fonda 1974). Valley walls extend approximately 60 m from either side of the valley floor up to the broad glacial outwash terrace (plateau). A majority of the valley floor and valley walls are within the ONP Queets corridor, whereas the plateaus are within Washington Department of Natural Resources (DNR) and Olympic National Forest (ONF) lands.

Climate is maritime with mild, wet winters and cool, dry summers. Annual rainfall averages approximately 300 cm, with the majority falling between October and May. Snowfall occurs infrequently and accumulation rarely exceeds 30 cm. Abundant rainfall, moderate temperatures, and coastal fog have created a temperate rain forest ecosystem in the Queets Valley and the three other major river drainages on the west side of the Olympic Mountains (Franklin and Dyrness 1973). Winter temperatures from 1 January-10 February, 1987 in forested and nonforested habitats of the plateau were not significantly different than those on the valley floor.

Vegetation of the valley floor represents seral stages of the *Picea sitchensis* vegetation zone (Franklin and Dyrness 1973), which are associated with the age of alluvial terraces, soil moisture, and soil profile (Fonda 1974). Active river channels that receive frequent fluvial disturbance support pioneer deciduous forests (<10 years old) dominated by red alder (*Alnus rubra*) and willows (*Salix* spp.). The youngest alluvial terraces above the active channels support mature deciduous forests (>10 years old) dominated by red alder, black cottonwood (*Populus trichocarpa*) and bigleaf maple (*Acer macrophyllum*). Mid-seral coniferous/deciduous forests occur on mid-aged alluvial terraces and are dominated by spruce, black cottonwood (*Populus tremuloides*) and bigleaf maple (*Acer macrophyllum*) (Fonda 1974). Old-age coniferous forests (>150 years old), dominated by Sitka spruce and western hemlock (*Tsuga heterophylla*), occur commonly on the oldest alluvial terraces of the valley floor. Approximately 30 percent of mature forests was selectively logged between 1910 and 1945. The corridor now consists of dense, coniferous forests (30-150 years old) comprised predominantly of Sitka spruce and western hem-

lock. Vegetation of the valley floor also includes 55 abandoned homestead clearings that range in size from 2 to 16 ha and are composed primarily of non-native grasses.

Vegetation of the adjoining glacial plateau is characteristic of the *Tsuga heterophylla* forest zone of western Washington (Franklin and Dyrness 1973). Unharvested old-age stands of western hemlock (>150 years old) cover approximately 11 percent of their original distribution on the glacial plateau. The remaining forests have been converted to 1-150 year-old, even-aged forests by clear-cutting and planting of nursery seedlings, or by wildfire. One to 15 year-old clearcuts are dominated by non-native grasses and forbs, as well as shrubs, including huckleberries and *Rubus* spp., and regenerating conifers. The majority of clear-cuts were planted with Douglas-fir (*Pseudotsuga menziesii*) or western hemlock seedlings, with some areas containing dense stands of naturally seeded western hemlock. The percent cover of coniferous trees in stands 16-30 years old is 100 percent, and the coniferous cover in stands 31-150 years old is 94 percent (G. L. Schroer, Nat. Park Serv., unpubl. data).

No hunting is allowed within ONP, but hunting for elk, deer, bear, and other species is permitted on other federal, state, and private lands adjacent to the park. Annual legal elk harvests from the western Olympic Peninsula averaged $0.22 + 0.03$ (SE) elk/km² from 1983 to 1987 (Houston *et al.* 1990).

Methods

We placed radio-collars on 1-2 adult female elk in 4 of 5 herds inhabiting the study area. Elk were immobilized with mixtures of Carfentanil or M99 (etorphine) and Rompun (xylazine). Movements of adult females and calves within a herd are highly interdependent on the Olympic Peninsula (Jenkins and Starkey 1982, Schroer 1987); therefore, locational data from only 1 adult female in each of the 4 herds was used in the analysis.

The 4 herds monitored were referenced according to regional features in each area: Kelly (K), Streater (S), Tacoma (T), and Higley (H). The herd sizes were approximately 30 (K); 45 (S); 70 (T) and 35 (H). The elk were studied during 5 seasons: summer (27 June-14 September 1986); autumn (15 September-3 December 1986); winter (7 December 1986-15 February 1987); spring (25 February-19 May 1987); and calving (20 May-

20 June 1987). An adult female of the Streater herd was not radio-collared until early summer; therefore, it was not included in the summer data.

We relocated elk by first obtaining a general location by using radio-telemetry and then by approaching to confirm a visual sighting or aural location. Locations were not recorded if elk were disturbed prior to detection. In 7 percent of the relocations, we used remote triangulation procedures to locate elk from distances of 150-1,000 m. Average location errors derived from field tests at those distances were 110 meters. All locations were recorded according to 100 m coordinates of the Universal Transverse Mercator System. Data from remote triangulation were used in assessing vegetation selection patterns only if the error polygon was completely within a single vegetation class.

Vegetation selection patterns were determined by locating each elk once or twice daily on random days and at random times between dawn and dusk 3-5 days per week. To help ensure that locations from the same day were independent, successive locations were separated by a minimum of three hours. A minimum of three hours was a sufficient period for the elk to change activity or vegetation class in greater than 50 percent of consecutive locations within a day.

Individual patterns of vegetation selection were examined by comparing proportional use of vegetation classes to proportional availabilities of vegetation classes within annual home ranges of individual elk. Annual home ranges were delineated using 100 percent contour intervals of the harmonic mean utilization distribution (Dixon and Chapman 1980) using the computer program McPAAL (Stuwe and Blohawiak 1985). Vegetation classes were mapped within home ranges on 1:24,000 scale base maps using aerial photographs, DNR and ONF timber management maps, orthophotographs, and field verification. Availabilities of vegetation classes were measured using a digital planimeter.

We tested null hypotheses that elk used vegetation classes in proportion to availability using Chi-square tests and family confidence intervals based on Bonferroni Z-statistics (Neu *et al.* 1974). A vegetation class was considered selected when proportional use exceeded availability (family-level $P \leq 0.05$), and was considered avoided when use was less than availability. Statistical tests could not be conducted when there was no documented use of an available habitat type or topographic area, although those types or areas were considered

avoided. Vegetation habitat use could not be statistically determined for calving season due to the small sample size and large number (12) of habitat types (Koehler and Lantz 1980).

Results

Radio-collared elk selected the valley floor during all seasons except winter (Table 1). During winter, elk generally used valley floor and plateau regions in proportion to availability.

During summer all radio-collared elk selected mature deciduous forests (>10 years old, Table 1). Additionally, collared elk tended to select coniferous/deciduous forests and old homestead fields, although those trends were significant for only one of three collared elk. All collared elk avoided 31-150 year-old conifer stands on the valley floor, and also 1-5 and 16-150 year-old conifer stands on the plateau. Old-age (>150 years old) Sitka spruce forests on the valley floor were used in proportion to availability, but old-age western hemlock forests on the plateau were avoided during summer.

Each of the radio-collared elk continued to select mature deciduous forests (>10 years old) throughout autumn (Table 1). Additionally, 3 of 4 elk selected conifer/deciduous and old-age spruce forests on the valley floor. All seral stages available to elk on the plateau were generally avoided during autumn.

During winter, all radio-collared elk selected 6-15 year-old conifer stands on the plateau (Table 1). Increased use of 6-15 year-old stands corresponded with decreased use of mature deciduous forests (>10 years old) and conifer/deciduous forests on the valley floor. Two of four elk continued to select old-age spruce forests on the valley floor during winter. Elk tended to avoid 1-5 and 16-150 year-old coniferous stands on the valley plateau, and they generally used old-age western hemlock forests in proportion to availability.

During spring, elk use of 6-15 year-old forests diminished while use of mature deciduous forests (>10 years old), conifer/deciduous forests, and old homestead fields increased on the valley floor (Table 1). Elk used old-age spruce forests on the valley floor in proportion to availability during spring, and avoided 1-5 and 16-150 year-old conifers on the plateau.

Although selection patterns could not be evaluated statistically during the short calving season, use of conifer/deciduous forests on the valley floor

TABLE 1. Percent availability and use of physiographic zones and vegetation classes by adult female Roosevelt elk from 4 herds in the Queets River Valley, Washington.

Physiographic Zone/ Vegetation Class	Availability (% of annual home range)				Use ^{1,2,3} (% of locations)																Calving ⁴			
					Summer			Autumn			Winter				Spring									
					27 Jun– 14 Sep			15 Sep– 3 Dec			7 Dec– 15 Feb				25 Feb– 19 May									
	K	S	T	H	K (58)	T (60)	H (61)	K (67)	S (69)	T (69)	H (70)	K (64)	S (63)	T (63)	H (64)	K (58)	S (59)	T (57)	H (58)	K (27)	S (31)	T (27)	H (31)	
Valley Floor ⁵																								
Deciduous Forest < 10 yrs	1	1	1	1	0-	2- ³	0-	3	0-	3	0-	0-	0-	0-	0-	2	0-	0-	0	14	0	0		
Deciduous Forest > 10 yrs	3	19	7	8	38+	44+	32+	32+	50+	40+	31+	18+	17	12	0-	47+	44+	58+	31+	12	5	44	5	
Coniferous/Deciduous Forests	10	8	11	8	26+	23	21	28+	10	28+	29+	14	11	13	13	16	10	28+	32+	39	24	17	25	
Coniferous Forest 31-150 yrs	19	11	13	10	7-	5-	7-	10-	7	9	3-	6-	10	6	6	5-	0-	0-	5	0	0	3	0	
Coniferous Forest > 150 yrs	2	9	7	1	12	10	13	20+	23+	13	15+	5	22+	10	14+	3	12	2	3	27	47	11	19	
Old Homestead Field	1	1	1	1	16+	0-	0-	7	10	7	7	5	5	3	0-	29+	29+	5	5	22	5	11	9	
Other	3	3	1	1	2	0-	0-	0-	0-	0-	0-	0-	0-	2	0-	0-	0-	2-	0	0	0	0		
Habitats on the Plateau ⁶																								
Coniferous Forest 1-5 yrs	10	4	11	20	0-	0-	0-	0-	0-	0-	3-	0-	0-	5	3-	0-	0-	0-	5-	0	0	0	0	
Coniferous Forest 6-15 yrs	9	12	15	7	0-	15	23+	0-	0-	0-	9	43+	32+	38+	56+	0-	3-	7	17	0	0	0	0	
Coniferous Forest 16-30 yrs	17	12	4	12	0-	0-	3-	0-	0-	0-	3-	3-	0-	3	0-	0-	0-	0-	0	5	14	42		
Coniferous Forest 31-150 yrs	19	9	11	19	0-	0-	0-	0-	0-	0-	0-	2-	0-	2-	0-	0-	0-	0-	0	0	0	0		
Coniferous Forest > 150 yrs	5	11	19	14	0-	0-	2-	0-	0-	0-	0-	3	3-	6	8	0-	0-	0-	0-	0	0	0	0	

¹ Herds designated by (K) Kelly; (S) Streater; (T) Tacoma and (H) Higley.² Total number of locations are indicated in parentheses.³ "+" and "-" indicate use significantly greater or less than availability, respectively, based on family confidence intervals using Bonferroni Z statistics, $P < 0.05$ (Neu *et al.* 1974).⁴ Percentages of use were not statistically compared with percentages of availability during calving season due to the small sample size.⁵ Coniferous forests on valley floor are predominantly the sitka spruce (*Picea sitchensis*) vegetation zone (Franklin and Dyrness 1973).⁶ Coniferous forests on plateaus are predominantly the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1973).

and 16-30 year-old conifer stands on the plateau appeared to increase during calving (Table 1). Use of old-homestead fields and old-age spruce forests remained high during calving, whereas use of mature deciduous forests (> 10 years old) decreased. Use of 1-5 year-old, 16-150 year-old, and old-age conifer stands on the plateau remained low during calving.

Discussion

Valley bottoms and riparian areas along the Queets River were key habitats selected by elk year around. Mature deciduous forests and coniferous/deciduous stands appeared to be important foraging areas of elk during all seasons except winter. In general, deciduous forests contain abundant forage for elk in comparison to coniferous forests of similar ages (Franklin and Pechenac 1968). Mature deciduous forests in our study area contained > 95 percent ground cover (G. L. Schroer, Nat. Park Serv. unpubl. data) of important elk forages in the region (Leslie 1982). Research of other elk populations in western Washington and Oregon and Vancouver Island, B.C. also documented elk selection of deciduous forests and riparian areas (Brunt *et al.* 1989, Cooper 1988, Schroer 1987, Jenkins and Starkey 1984, Witmer and deCalesta 1983).

Even-aged coniferous stands less than 150 years old received little use by elk, except during winter, when 6-15 year-old clearcuts were selected by all elk. Stands that were 6-15 years old contained the most abundant forage (78% ground cover) of any even-aged coniferous stands less than 150 years old (G. L. Schroer, Nat. Park Serv. unpubl. data), which might have contributed to their selection. Coniferous stands approximately 10-25 years old in southeast Alaska also had the greatest abundance of forage cover of all seral stages (Alaback 1982). The habitat benefits of 6-15 year-old coniferous stands, however, are short-lived. Only 10-15 percent of a 60-90 year cutting cycle would include that age class. Succession of young coniferous stands to pole-sized and mature stands reduces forage quantity, and typically those stands persist for approximately 75 years (83%) of a 90-year cutting cycle.

The majority of radio-collared elk selected old-age spruce forests on the valley floor during autumn and winter, and generally avoided old-age western hemlock forests on the plateau except during winter. Reasons for the discrepancy among selection of these old-age habitat types are not clear

from our data, but undoubtedly they stem from differences in landscape patterns and forage productivity in the two physiographic zones. Proximity of old-age Sitka spruce forests to preferred deciduous forests in the valley floor may have enhanced use of those conifer stands in bottomlands. Additionally, although we did not attempt to measure differences in forage abundance among old-age forest associations in the Queets Valley, cover of preferred forages of elk differed appreciably among climax forest associations in the nearby Hoh Valley (Smith and Henderson 1985). Other habitat benefits attributed to old-age forests include: snow interception and associated energetic benefits during winter (Jones 1974, Harestad *et al.* 1982, Parker *et al.* 1984, Zahn 1985); greater nutritional quality of browse (Happe *et al.* 1990), and abundant forage (Alaback 1982). Additional research clearly is needed to determine influences of site quality, forage production, and forest structural characteristics on elk habitat attributes and selection among old-age forest associations.

Management Implications

Conversion of old-age coniferous forests in many areas of the Pacific Northwest has created extensive even-aged stands less than 90 years old that are avoided by elk. Timber management projections indicate that by the year 2030, more than 65 percent of the total area of commercial forest lands in western Washington and Oregon will be between the ages of 30 and 90 years old (Harris 1984), and old-age coniferous forests will cover less than 10 percent of their original area (Franklin *et al.* 1981, Harris 1984).

The increasing prevalence of 16-90 year-old even-aged stands poses a significant problem for management of some elk ranges in the Pacific Northwest. Extensive even-aged coniferous forests generally do not contain the interspersed forage and cover areas recommended by elk managers (Witmer *et al.* 1985). We recommend that comprehensive management plans be developed on a watershed or sub-watershed basis, including state, private, and federal lands, to ensure long term availability of preferred elk habitats within the managed forest.

Forest management in valley floor and riparian areas should be conducted in a manner that protects and enhances preferred vegetation habitats, especially mature deciduous forests which are key habitats for elk during most seasons. Old-age coniferous bottomland forests should also be

protected on critical autumn and winter ranges. Where old-age forests cannot be retained or re-established, uneven-aged management with lengthy cutting rotations of over 150 years may be required to recreate a favorable interspersed cover and forage.

Many additional silvicultural practices such as non-commercial and commercial thinning, shelterwood cuts and small patch-cuts (i.e., 1-5 acres) have also been proposed as means of improving habitat interspersed and forage production in second-growth, even-aged forests (Bunnell and Eastman 1976, Hall *et al.* 1985, Witmer *et al.* 1985). Precommercial thinning, however, is typically not effective in improving forage availability for elk, because resulting slash depths often inhibit understory production and elk movements (Garrison and Smith 1974, Bunnell and Eastman 1976). Additionally, precommercial thinning of younger stands typically opens overstory canopies and increases forage cover for only relatively short periods (i.e., 5-10 years) depending on the number

of trees removed (Hungerford 1969, Bunnell and Eastman 1976). Uneven-aged management and commercial thinning have been used effectively on the Olympic Peninsula to create foraging areas within the even-aged forest (M. Stoll, Olympic Nat. For., pers. comm., 1991). Additional silvicultural prescriptions that maintain partial openings in the overstory canopy in even-aged stands and produce acceptable quantities of slash debris need to be developed and implemented.

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Literature Cited

- Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63:1932-1948.
- Brunt, K., D. Q. Becker, and J. A. Youds. 1989. Vancouver Island Roosevelt elk/intensive forestry interactions: Phase 1 (1981-1986) Job compl. report. Res. Min. of Envir. & Forests, IWIFR-33, No. B-51. Victoria, British Columbia.
- Bunnell, F., and D. Eastman. 1976. Effects of forest management practices on wildlife in the forests of British Columbia. In *Proc. XVII IUFRO World Congress, Div. 1*. Pp. 631-689.
- Cooper, K. C. 1988. Seasonal movements and habitat use of migratory Roosevelt elk in Mount Rainier National Park. Oregon State Univ., Corvallis. M.S. Thesis.
- Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040-1044.
- Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology* 55:927-942.
- Franklin, J. F., and A. A. Pechanec. 1968. Comparison of vegetation in adjacent alder, conifer and mixed alder-conifer communities: understory vegetation and stand structure. In J. M. Trappe (ed.) *Biology of Alder*. U.S.D.A. For. Serv., Portland, OR. Pp. 37-44.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-8.
- Franklin, J. F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-118.
- Franklin, J. F., and T. A. Spies. 1984. Characteristics of old-growth Douglas fir forests. In *New Forests For a Changing World*. Proc. of the 1983 Soc. Amer. Foresters Nat. Conv., Portland, OR. Pp. 10-16.
- Garrison, G. A., and J. G. Smith. 1974. Habitat of grazing animals. In O. Cramer (ed.) *Environmental effects of forest residues in the Pacific Northwest*. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-24. Pp. 1-10.
- Hall, C. F., C. McComb, and W. Ruediger. 1985. Silvicultural options. In E. R. Brown (ed.) *Management of wildlife and fish habitats in forests of western Oregon and Washington*. U.S.D.A. For. Serv., Pub. No. R6-F&WL-192-1985. Pp. 291-306.
- Happe, P. J., K. J. Jenkins, E. E. Starkey, and S. H. Sharrow. 1990. Nutritional quality and tannin astringency of browse in clear-cuts and old-growth forests. *J. Wildl. Manage.* 54:557-566.
- Harestad, A. S., J. A. Rochelle, and F. L. Bunnell. 1982. Old-growth forests and black-tailed deer on Vancouver Island. *Trans. N. Amer. Wildl. Conf.* 47:343-352.
- Harris, L. D. 1984. *The Fragmented Forest—Island Biogeography Theory and the Preservation of Biotic Diversity*. Univ. of Chicago Press, Chicago.
- Harris, L. D., C. Maser, and A. McKee. 1982. Patterns of old-growth harvest and implications for Cascades wildlife. *Trans. N. Amer. Wildl. Nat. Res. Conf.* 47:374-392.
- Houston, D. B., E. G. Schreiner, B. B. Moorhead, and K. A. Krueger. 1990. Elk in Olympic National Park: will they persist over time? *Nat. Areas J.* 10 (1):6-11.
- Hungerford, K. E. 1969. Influences of forest management on wildlife. In H. C. Black (ed.) *Proc. wildlife and forestation in the Pacific Northwest*. School of For., Oregon State Univ., Corvallis. Pp. 39-41.

- Jenkins, K. J., and E. E. Starkey. 1982. Social organization of Roosevelt elk in an old-growth forest. *J. Mammal.* 63:331-334.
- . 1984. Habitat use by Roosevelt elk in unmanaged forests of the Hoh Valley, Washington. *J. Wildl. Manage.* 48:642-646.
- Jones, G. 1974. Influence of forest development on black-tailed deer range on Vancouver Island. In H. C. Black (ed.) *Wildlife and forest management in the Pacific Northwest*. School of For., Oregon State Univ., Corvallis. Pp. 139-148.
- Juday, G. P. 1977. Location, composition and structure of old-growth forests of the Oregon Coast Range. Oregon State Univ., Corvallis. Ph.D. Thesis.
- Koehler, K. J., and K. Larntz. 1980. An empirical investigation of goodness-of-fit statistics for sparse multinomials. *J. Amer. Stat. Assoc.* 75:336-344.
- Leslie, D. M. 1982. Nutritional ecology of cervids in old-growth forests in Olympic National Park, Washington. Oregon State Univ., Corvallis. Ph.D. Thesis.
- Meslow, E. C., C. Maser, and J. Verner. 1981. Old-growth forests as wildlife habitat. *N. Amer. Wildl. Nat. Res. Conf.* 46:329-325.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541-545.
- Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manage.* 48:474-488.
- Schroer, G. L. 1987. Seasonal distribution and movements of migratory Roosevelt elk in the Olympic Mountains, Washington. Oregon State Univ., Corvallis, OR. M.S. Thesis.
- Schroer, G. L., G. Witmer, and E. E. Starkey. 1988. Effects of land use practices on Roosevelt elk winter ranges, Western Washington and Oregon. In M. Zahn, J. Pierce, and R. Johnson (eds.) *Proc. Western States and Provinces Elk Workshop*, Wash. Dept. of Wildl. Pp. 68-74.
- Smith, B. G., and J. A. Henderson. 1985. Baseline vegetation survey of the Hoh and Dosewallips drainages, Olympic National Park, Washington. Final Report, Olympic National Park, Port Angeles, Washington.
- Stuwe, M. and C. Blohawiak. 1985. Microcomputer programs for the analysis of animal locations. Conservation and Research Center, Nat. Zool. Park, Smithsonian Institute.
- Tabor, R. D. 1975. Guide to the geology of Olympic National Park. Pac. N.W. Nat. Parks and For. Assoc.
- Witmer, G. W., and D. S. deCalesta. 1983. Habitat use by Roosevelt elk in the Oregon Coast Range. *J. Wildl. Manage.* 47:933-939.
- . 1985. Effect of forest roads on habitat use by Roosevelt elk. *Northw. Sci.* 59:122-125.
- Witmer, G. W., M. Wisdom, E. P. Harshman, R. J. Anderson, C. Carey, M. P. Kuttel, I. D. Luman, J. A. Rochelle, R. W. Scharpf, and D. Smithey. 1985. Deer and Elk. In E. R. Brown (ed.) *Management of wildlife and fish habitats in forests of western Oregon and Washington*. U.S.D.A. For. Serv., Pub. No. R6-F&WL-192-1985. Portland, OR. Pp. 231-259.
- Zahn, H. M. 1985. Use of thermal cover by elk (*Cervus elaphus*) on a western Washington summer range. Univ. Wash., Seattle. Ph.D. Thesis.

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Development of Oregon White Oak Seedlings

Abstract

Seedlings of Oregon white oak (*Quercus garryana* Dougl. ex Hook.) growing in western Oregon developed a multi-stemmed morphology that persisted for many years before shifting to a form dominated by a single stem (a sapling). These multi-stemmed seedlings were up to 56 cm tall and had one to six stems ranging in age from 1-9 years; several ages of stems usually were present on one plant. Height growth per seedling averaged 4.6 cm per year; taproot growth averaged 7.3 cm per year. Stem death averaged 8 percent per year; new stems were produced at a rate of 0.2 stems per plant per year and were closely associated in time with stem death on the same plant. The change from seedling to sapling morphology appeared to be rapid; sapling height growth averaged 15.7 cm per year for the single dominant stems. Root systems of saplings averaged 13 years older than the dominant stem; in one plant the difference was 42 years.

The causes of the prolonged seedling phase and subsequent shift in morphology and growth rate are not clear. Browsing by sheep and deer did not contribute to the prolonged multi-stemmed phase; little evidence of browsing was found. The shift to the sapling phase did not appear to be related to moisture availability; we could find no difference in predawn plant water potential between seedlings and saplings.

Introduction

Oregon white oak (*Quercus garryana* Dougl. ex Hook.) is found on dry sites from southwest coastal British Columbia to northern California. Today, this species occurs in forest stands and in woodlands where the trees are scattered throughout a grass matrix (Morris 1934, Habeck 1961, Thilenius 1968). Regeneration is rare (Sprague and Hansen 1946, Habeck 1961, Thilenius 1968, Johannesen *et al.* 1971), as has been found generally for oaks in Mediterranean climates (Griffin 1976). The largest populations of Oregon white oak are found in western Oregon, particularly in the valleys drained by the Willamette River and its tributaries.

Very little is known about the regeneration of Oregon white oak and, in particular, about seedling survival and growth. *Silvics of North America* (U.S. Forest Service 1990) describes initial shoot growth as slow and root growth as rapid. Cole (1977) reported what he described as stunted seedlings on ridges and upper slopes at the south end of the Willamette Valley. Our early observations did reveal many small oaks with multiple stems and a shrubby appearance; these may be equivalent to Cole's (1977) stunted seedlings.

Other oak species and close relatives commonly pass through a seedling stage characterized by multiple stems, frequent stem death, and the development of a root system older than the aboveground parts (Merz and Boyce 1956, Hibbs 1983, Tappeiner and McDonald 1984, Tryon and Powell 1984). Such observations led to the formal definition of a seedling sprout as a seedling that has a

root collar diameter less than 5 cm and a root system that is older than the aboveground growth (Society of American Foresters 1950).

The causes for such a developmental process have not been explored. Tryon and Powell (1984) described a dieback of oak seedling sprouts in West Virginia as resulting from "suppression," although they did not elaborate further. The eastern oaks, however, differ from Oregon white oak in that they regularly occur in light-limited environments. Under these conditions, dieback of stems can result from the respiratory requirements of larger (older) stems exceeding photosynthesis. Most of the Oregon white oak seedlings we have seen grow in open grasslands where light is not limiting.

Given the scarcity of information on Oregon white oak seedling survival and development, or even of good species for comparison, we undertook an initial investigation of this process and its underlying causes. We began with a characterization of the seedlings and, for comparison, small saplings. If Oregon oak seedlings could be characterized as seedling sprouts, then we wanted to know, first, how long they continued to die back and resprout; second, what characterized the transition from this stage to saplings; and, finally, what caused the transition. Research on California oaks (Griffin 1971, 1973, 1976) led us to expect that herbivory and drought could affect early growth.

Study Area

The study area, which included two adjacent sites (A and B), was in the west-central portion of the

Willamette River Valley, near Corvallis, Oregon. Soils were a clay loam in the Jory series. Depth to the highly fractured basalt bedrock was 100 to 200 cm. Precipitation averaged 1004 mm, with only 47 mm falling during June through August (Franklin and Dyrness 1973). The study area was representative of the *Quercus garryana*/*Rhus diversiloba* community type (Thilenius 1968).

Site A was on a west-facing hillside (10 to 40% slope) and consisted of open grasslands, oak woodlands and forests, and patches up to 0.5 ha of apparently even-aged oak seedlings. These seedlings were growing in open areas, usually where mature oaks had been harvested 15 to 25 years previously and where one to ten large trees per ha still remained. In our experience, this hillside was unusual because of the large amount of oak regeneration present there. We believe the soil disturbance caused by removal of mature oaks contributed to the high density of oak seedlings and saplings. Sheep have grazed the site annually for at least the past 15 years, and the area also contains a large deer herd. There was no evidence of a recent fire history.

Site B was used to provide an estimate of the duration of the seedling stage under a different disturbance regime. It was immediately west of Site A, but no history of logging activity was apparent at this site. Slope was slight (<5%). Soil type, grazing, and fire history were similar to those of Site A. Regeneration was scattered sparsely among widely spaced oak trees.

Methods

Characterization of Seedlings and Saplings

We began with the casual (non-quantitative) observation that the site contained a large number of oak plants of a shrubby form and a lesser number of plants with a more upright or tree-like form. In this paper we have defined seedlings as multiple-stemmed plants with no single dominant stem (plus single-stemmed recent germinants) and saplings as plants with a dominant stem. Sample plants were chosen to include the range of sizes present, but were restricted to plants with a minimum of aboveground competition. We did place an artificial upper limit of 2 m on height.

Twenty-three oak seedlings and 27 saplings were excavated from the study area. All 23 seedlings came from Site A. Nine of the saplings came from Site B. The root systems of oak seedlings and

saplings were excavated with shovels and trowels. Seedlings were excavated to a depth of 30 to 120 cm (wherever the taproot diameter diminished to 1 mm). Saplings were excavated to about 30 cm depth.

The number of live stems on all seedling samples was counted, heights and diameters of live stems were measured, and incidence of browsing was noted. Height and diameter (measured just above the root collar) were recorded for the dominant stem of each sapling. Taproot lengths and diameters were measured just below the root collar, and diameters were measured at 30-cm intervals along the root.

Stem and root ages were determined for all samples. We used ring counts to obtain above-ground ages. Seedling ring counts were cross-checked against counts of bud-scale scars from a subsample of 10 stems, and counts agreed to within 1 year. Stem ring counts were made at the base of live stems, just above the enlarged portion of the plant at the root-stem juncture (Figure 1). Belowground age was determined by counting rings in the taproot 2 cm below the ground and at 30-cm intervals along the taproot. Partial rings were observed, so we suspect missing rings; ring counts probably underestimate true belowground age.

Growth rates were calculated by dividing length (stem, total root, or root section) by the years required to grow the length. Root volume was calculated as the sum of the product of the length times the average of the cross-sectional area at the two ends of each 30-cm section.

Remeasured Seedlings

In the spring of 1987, 23 additional seedlings on Site A were permanently marked, and each stem was tagged and measured. Every spring (before leaf emergence) and fall (after leaf senescence) through spring of 1990, seedlings were relocated and stems remeasured. Stem length and basal diameter were measured, and incidence of damage (browse, dieback) was recorded. New stems were tagged and measured as they arose.

Water Potential

Predawn twig water potential (Ψ_{twig}) was measured from 20 pairs of seedlings and saplings at Site A. The members of each pair grew within 2 m of each other. Twig Ψ was also measured on large trees distributed throughout the study area. Measurements

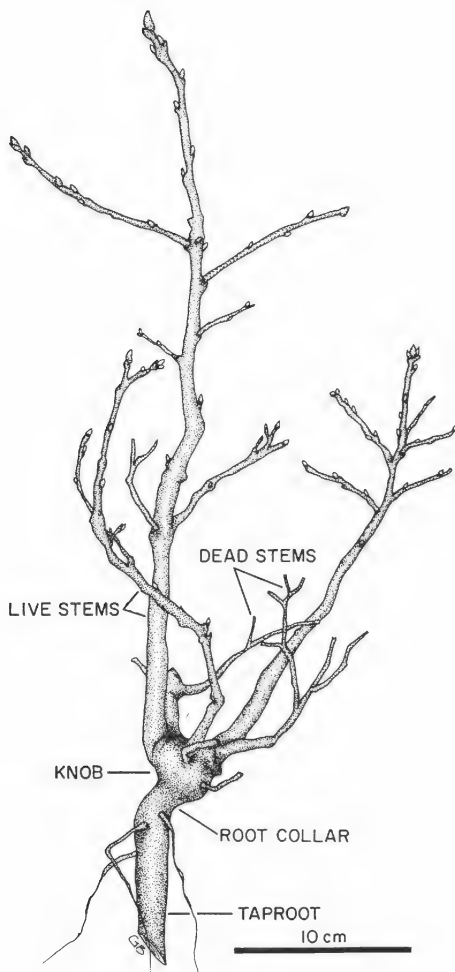


Figure 1. Drawing of the features common to older, multi-stemmed seedlings of Oregon white oak: a taproot, a knob at the top of the root, and live and dead stems.

were taken with a portable pressure chamber between 3 and 5 a.m. on August 22, 1985, and July 3 and 29, 1986. The summers of 1985 and 1986 were similar in precipitation and water demand (Oregon State University Hyslop Farm record, unpub. data).

Results

Excavated Seedlings

Each sample had one to six stems 2–56 cm tall; we found no plants more than 56 cm tall that met our morphological definition of a seedling. Most stems originated from the enlarged knob above the root collar area at or near the soil surface, not from existing stems (Figure 1). Although some seedlings had belowground ages of up to 21 years, individual stem ages averaged 4.6 years and never exceeded 9 years (Table 1). The maximum age span for the stems on any one plant was 7 years. All seedlings had stems more than 1 year old. Stem height growth averaged 4.6 cm/year.

Browsing is usually indicated by a missing distal end of a stem. This symptom was not seen on the excavated oaks, although other plant species at the site exhibited it; poison oak (*Rhus diversiloba* T. & G.), for example, was heavily browsed. However, apical meristems of white oak occasionally failed to grow, resulting in the growth of several lateral buds, producing a branchy appearance.

Each seedling had a single taproot with small laterals (diameter <0.5 mm) along its length. Taproot lengths averaged 56.3 cm, and diameters averaged 1.2 cm at a depth of 2 cm (Table 1). The taproots grew slowly, averaging 7.3 cm/year. The growth rate increased distally. Growth averaged 4.9 cm/year for the first 30 cm and increased to 7.7, 15.8, and 12.5 cm/year for the three subsequent 30-cm depth intervals.

Age of the seedling taproot ranged from 7 to 21 years, averaging 13.8 years (Table 1). Taproot diameter was strongly correlated with age (Pearson correlation, $r = 0.62$, $P < 0.05$) (Figure 2a); root volume was also strongly correlated with age ($r = 0.71$, $P < 0.01$).

Excavated Saplings

The average height of the dominant stem of each sapling was almost 1.2 m at Site A (Table 1); none was found to be less than 65 cm tall. Mean height growth was 15.7 cm/year. Sapling stem ages ranged from 3 to 17 years, averaging 7.5 years.

Whole root systems were not excavated for the saplings, but the taproot was still distinct at a depth of 30 cm. The average diameter of sapling taproots was 4.0 cm at a depth of 2 cm (Table 1). Lateral roots, which had diameters less than 1 cm, were commonly observed to depths of 30 cm. Taproot

TABLE 1. Characteristics of excavated Oregon white oak seedlings and saplings grown in western Oregon (Site A). Except for maximum ages, mean values are given. Standard deviations are shown in parentheses.

Sample	No. per plant	Length (cm)	Diameter* (cm)	Age (years)	Maximum age (years)	Height/depth growth (cm/yr)
Stems						
Seedlings n = 23	2.4 (1.4)	21.2 (13.3)	0.7 (1.2)	4.6 (2.0)	9	4.6
Saplings‡ n = 18	1	117.6 (32.5)	2.5 (1.0)	7.5 (3.9)	17	15.7
Taproots						
Seedlings n = 23	1	56.3† (30.7)	1.2 (0.5)	13.8 (4.4)	21	7.3†
Saplings n = 18	1	—	4.0 (1.3)	20.2 (5.0)	28	—

*Just above (for stems) or below (roots) the root collar.

‡For tallest stem only.

†n = 16 (not all seedling root systems were excavated to their distal end).

age of the saplings varied from 12 to 28 years, averaging 20.2 years. For saplings alone, taproot age and diameter were not correlated ($P > 0.05$). However, for combined seedling and sapling data, root age and diameter were correlated ($r = 0.69$, $P < 0.01$) (Figure 2a). The maximum difference between above- and belowground ages at Site A was 21 years.

The saplings from Site B had an average stem age of 42.0 years, with a maximum of 60 years. Taproot age ranged from 55 to 72 years and averaged 64.8 years. Regeneration at this site is clearly older than that at Site A. The maximum difference between above- and belowground ages at Site B was 42 years.

Seedling/Sapling Comparisons

Reconstructing the growth history of saplings showed that oak seedlings undergo a prolonged period of dieback and resprouting before producing a stem that grows into a sapling. Figure 2 further characterizes these two morphological stages in a form that facilitates comparison of the stages and an examination of the transition. Note that we sampled all sizes of both seedlings and saplings.

Figure 2a portrays a developmental continuum between the two stages. There is no jump in size between seedling and sapling stages; the transition is smooth. Although all saplings were taller than all seedlings (Figure 2b), seedlings and saplings overlapped widely in height growth rate. Among

the seedlings there are many slow-growing stems; none of the sapling stems grew as slowly as the slowest seedling stems. Some seedling stems had high growth rates, similar to those of the fastest saplings, but these plants were short and still had the morphology of the seedling stage.

Figure 2c, showing plant age vs. stem growth, elaborates these points. Here, only the tallest stem of each plant is included. Seedlings and saplings overlapped widely in age (Figure 2c). Except for the two fast-growing seedlings, there was a clear delineation between seedlings and saplings. The two aberrant plants are seedlings morphologically; functionally, they are behaving like saplings and may soon have the appearance of a sapling.

Seedling Population Dynamics

In 3.5 years, three of the 23 remeasured seedlings died; each had had its tap root severed by pocket gophers. A total of 78 stems on 23 seedlings (average = 3.4 stems/plant) were censused during this period. Of these, 22 died—15 during the winter and 7 during the summer. During any one measurement period, no more than one stem on a plant died. Stems that died tended to be among the smaller on a plant. During the census period, 16 new stems were produced. Plants on which stems died and plants that produced new stems had similar numbers of stems per plant (4.6 and 5.0), but had significantly more stems than other plants ($P \leq 0.05$). Only two incidences of stem production

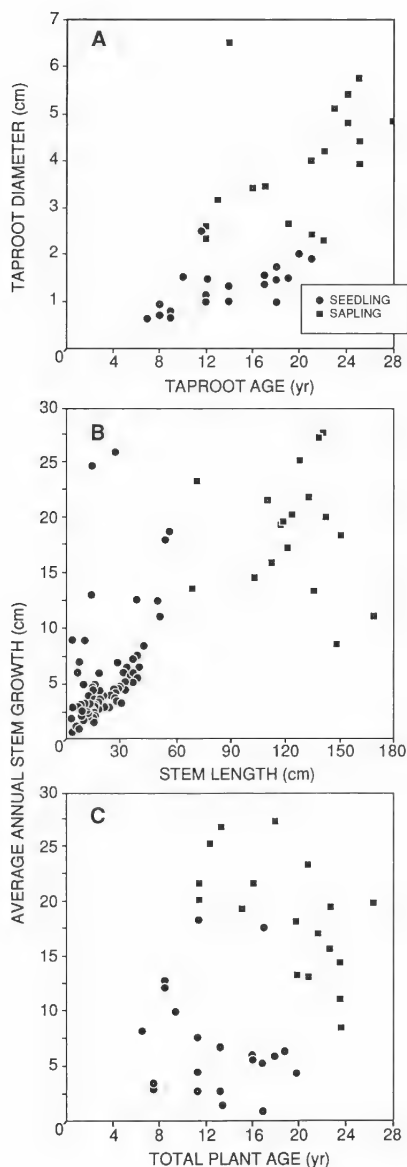


Figure 2. Seedling and sapling size and growth. A. Taproot age and diameter (taken just below the soil surface). Note that there is little overlap in diameter between the two morphological classes. B. Stem length and growth, showing large overlap in stem growth rate between the two morphological groups (includes all seedling stems). C. Plant age and stem growth, showing separation between seedlings and saplings in growth and age characteristics (includes only the tallest seedling stem).

occurred on plants not experiencing stem death, and four stems died on plants that were not producing new stems.

Nine incidences of browsing were found during 3.5 years. In addition, four stems exhibited partial dieback from the top at some point during the study period. Browsing was more common during the winter; dieback was more common during the summer. Most of the summer stem mortality occurred during only one of the three summers (1988).

Stem diameter increased through the three growing seasons (Table 2). Average height of live stems varied, although height growth appeared to increase with time.

TABLE 2. Stem diameter and height growth of 23 white oak seedlings.

Year	N	Size of stems alive at beginning of growing season		N	Growth of stems alive at beginning and end of growing season	
		Diameter (mm)	Height (cm)		Diameter growth (mm/yr)	Height growth (cm/yr)
1986*	64	5.4	33.8	—	—	—
1987	61	6.0	34.7	60	0.46	0.1
1988	60	6.3	31.5	47	1.08	1.4
1989	56	7.4	38.1	55	0.85	4.7

*Based on measurements taken in spring 1987.

Twig water potential (Ψ_{twig})

Water potential did not differ between seedlings and saplings at any date (paired t-test, $P < 0.01$) (Table 3). Tree water potential was significantly ($P \leq 0.05$) greater at the late-season date (August 22) than were seedling and sapling water potentials.

TABLE 3. Predawn twig water potential for seedling, sapling, and tree samples of Oregon white oak.

Date	Seedlings (-mPa)	Saplings (-mPa)	Trees (-mPa)
August 22, 1985	1.86 a	1.87 a	0.69 bc
July 3, 1986	0.40 c	0.37 c	0.38 c
July 29, 1986	1.05 b	0.95 bc	0.74 bc

NOTE: Values followed by the same letter are not significantly different ($P < 0.05$, Scheffé's range test). N = 20 except Trees, where N = 10 for August 22, 4 for July 3, and 6 for July 29.

Discussion

The initial morphological distinctions that we made between seedlings and saplings have been supported and augmented by measurements of size and growth (Figure 2). While the age ranges of seedlings and saplings overlapped greatly, seedlings were generally smaller and grew more slowly; saplings were taller and grew faster. The few seedlings with high growth rates appear to be in the transition between the two classes; with such high rates of growth, they are unlikely to retain the appearance of seedlings for long.

After germination, Oregon white oak seedlings develop a multi-stemmed morphology that can persist for more than 20 years as stems repeatedly die back to the ground and new stems sprout. These plants fit the definition of seedling sprouts (Society of American Foresters 1950), although they support an unusually large number of stems. The root system, especially the taproot, expands throughout this stage.

New stems are continually produced, averaging 0.2 stems per plant per year, but browsing does not appear to be an important factor regulating their growth. In spite of the regular presence of sheep and deer, little browsing was observed. Partial dieback of stems also appears unimportant; its incidence was low. The cause of this partial dieback is not clear but may include insects and water stress.

Stem death is common; 22 of 78 stems died in 3.5 years, a death rate of 8 percent per year. The causes of death are not clear. Only one of the several stems on a plant died in any given measurement period. Because the stems that died were among the smallest stems on the plants, self-shading is a possible cause. However, these seedlings are growing in a high light environment and have shallow crowns. It seems unlikely that self-shading would be sufficiently intense to cause mortality; perhaps carbohydrate shortages induced by moisture stress are a more likely cause.

All recorded seedling death was caused by pocket gophers. We have not been successful at putting this in an historical context; we could find no reports of early gopher population densities. Populations of gopher predators are low today, so gopher populations may be higher now than in the past.

While Figures 2a and 2b suggest a continuum of some characteristics between plants with seed-

ling and sapling morphologies, Figure 2c shows a distinction in terms of age and growth. The scarcity of plants falling into a transitional condition indicates that the transition was probably fairly rapid. The more vigorous growth of stems of saplings than seedlings (15.7 vs. 4.6 cm/yr) shows how the multiple-stemmed seedlings can change into single-stemmed trees; one stem dominates and outgrows the rest. For several years, the remnants of the other stems can be seen at the base of new saplings.

The cause of this transition is still unclear. Browsing was found to be too uncommon to maintain seedlings in a multi-stemmed form. The primary alternative external factor regulating growth is moisture availability (Griffin 1971, 1973, 1976). As the root system of a seedling develops, its ability to capture moisture improves; if it survives, the seedling eventually taps deep water reserves that ultimately change its growth rate. However, we could document no differences in predawn twig water potential between seedlings and saplings and so could not support the hypothesis that water availability regulated the shift in growth pattern. Larger trees, however, apparently can utilize moisture reserves not available to seedlings or saplings. The patterns and ranges we found for predawn Ψ_{twig} are similar to those found for young California oaks (Griffin 1973, Baker *et al.* 1981), which grow in a region with a similar though drier climate pattern.

The pattern of early development of Oregon white oak has much in common with other oak species. However, an unusual feature of this species is its utilization of a multi-stemmed (seedling sprout) phase even though light is not a limiting environmental factor. We were not able to show that browsing or moisture availability was associated with the shift in morphology from multi-stemmed to single-stemmed sapling form. This shift might be regulated by an internal factor such as carbon storage. Such a mechanism would be an adaptation for building fire resistance quickly, once large investments in aboveground biomass begin. The levels of moisture availability observed in this study indicate that seedling growth is probably moisture limited, and moisture also may be important to individual stem mortality.

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Literature Cited

- Baker, G. A., P. W. Rundel, and D. J. Parsons. 1981. Ecological relationships of *Quercus douglasii* (Fagaceae) in the foothill zone of Sequoia National Park, California. *Madroño* 28:1-12.
- Cole, D. 1977. Ecosystem dynamics in the coniferous forest of the Willamette Valley, Oregon, U.S.A. *J. Biogeogr.* 4:181-192.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
- Griffin, J. R. 1971. Oak regeneration in the upper Carmel Valley, California. *Ecology* 52:862-868.
- . 1973. Xylem sap tension in three woodland oaks in central California. *Ecology* 54:152-159.
- . 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. *Amer. Midl. Nat.* 95:422-435.
- Habeck, J. R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. *Northw. Sci.* 35:65-77.
- Hibbs, D. E. 1983. Forty years of forest succession in central New England. *Ecology* 64:1394-1401.
- Johannessen, C. L., W. A. Davenport, A. Millet, and S. McWilliams. 1971. The vegetation of the Willamette Valley. *Ann. Assoc. Amer. Geogr.* 61:286-302.
- Merz, R. W., and S. G. Boyce. 1956. Age of oak 'seedlings.' *J. For.* 54:774-775.
- Morris, W. G. 1934. Forest fires in western Oregon and western Washington. *Oreg. Hist. Q.* 35:313-339.
- Society of American Foresters. 1950. *Forest Terminology*. 2nd edition. Baltimore, Maryland.
- Sprague, F. L., and H. P. Hansen. 1946. Forest succession in the McDonald Forest, Willamette Valley, Oregon. *Northw. Sci.* 4:89-96.
- Tappeiner, J. C., II, and P. M. McDonald. 1984. Development of tanoak understories in conifer stands. *Can. J. For. Res.* 14:271-277.
- Thilenius, J. F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. *Ecology* 49:1124-1133.
- Tryon, E. H., and D. S. Powell. 1984. Root ages of advance hardwood reproduction. *For. Ecol. Manage.* 8:293-298.
- U.S. Forest Service. 1990. *Silvics of North America*. 2. Hardwoods. USDA Agric. Handb. 654.

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Influence of Soil Aluminum and pH on Armillaria Root Rot in Douglas-fir in Western Washington

Abstract

It was hypothesized that high extractable Al concentrations in acid soils in young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations in western Washington would induce root stress and increase susceptibility to Armillaria root disease. In contrast, however, soils from 5 to 35 year-old Douglas-fir stands with a high severity of Armillaria root disease (13-25 infected trees/ha) had significantly lower ($p < 0.05$) average water extractable Al concentrations ($9.0 \pm 3.1 \mu\text{g Al/g}$) than soils with low disease severity (0-12 infected trees/ha) ($22.4 \pm 5.3 \mu\text{g Al/g}$). Soil pH and 2N KCl extractable Al averaged 4.46 ± 0.10 and $313 \pm 164 \mu\text{g Al/g}$, respectively, in low severity sites and 4.73 ± 0.20 and $149 \pm 69 \mu\text{g Al/g}$, respectively, in high severity sites, but were not significantly different between low and high severity sites. To examine the specific effects of Al and pH, growth responses of isolates of *Armillaria ostoyae* (Romagn.) Herink from Douglas-fir plantations were examined in pure culture. Diameter growth on soil extract agar declined as water extractable Al increased. In addition, diameter growth decreased with increasing Al in non-buffered media. The separate effects of Al and pH, however, could not be determined with this experiment; Al levels ranged from 0-200 mg/L, but pH declined from 5.8 to 2.6. Diameter growth decreased rapidly with increasing Al levels in buffered media at pH 4, but less rapidly at pH 5 or 6. Without Al in the media *Armillaria* growth increased with decreasing pH. Both Al and pH influenced *Armillaria* growth in culture and had interacting effects.

Introduction

In the Pacific Northwest, *Armillaria* spp. causes the most common and widely distributed root disease of western conifers (Hadfield *et al.* 1986). Recent studies have shown *Armillaria* to consist of a complex of at least nine biological species in North America (Anderson 1986) with the pathogenic species on most conifers in the west thought to be *A. ostoyae* (Romagn.) Herink (Morrison *et al.* 1985, Wargo and Shaw 1985).

Although the factors that control pathogenicity of *Armillaria* have been widely studied, they are not well understood (Wargo and Shaw 1985). Because this fungus commonly attacks stressed trees, factors affecting both the vitality of the tree and the vitality of the fungus must be considered. General factors such as environmental stress (Wargo 1980) and habitat type (McDonald *et al.* 1987a, 1987b) have been related to the incidence of Armillaria root disease. Specific soil factors, such as nutrition and pH, may also be important (Wargo and Harrington 1991). Redfern (1978), Shields and Hobbs (1979), and Singh (1983) found that low soil pH favored disease development under field conditions, but this relationship was not clear in all studies (Redfern and Filip 1991).

High aluminum concentrations in acid soils cause plant stress and there has been much interest

in determining relationships between soil pH and Al toxicity to roots (Ulrich 1983). In the soil solution, Al occurs in a variety of ionic forms, such as Al^{3+} , $\text{Al}(\text{OH})^{2+}$ or $\text{Al}(\text{OH})_2^+$ (Parker *et al.* 1988). The most toxic form is assumed to be Al^{3+} , but it is generally in low concentrations in soil solutions because of low solubility. As soil pH is lowered Al becomes more soluble. Aluminum toxicity generally does not occur in soils with a pH above 5.5, but it becomes increasingly severe as the pH drops below 5 (Ulrich 1983).

In 1985 the authors noted that Armillaria root disease was killing young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees near Hoquiam, Washington in areas with relatively acid soil ($< \text{pH } 5$). It was hypothesized that high soil Al concentrations were causing root stress, thus making trees more susceptible to Armillaria root disease. There have been relatively few studies on the effects of Al on soil microbes and plant pathogens. However, it has been shown that soil Al can act as a fungitoxin (Ko and Hora 1972), and it can reduce soil pathogen levels (Hartley 1928, Orellana *et al.* 1975, Muchovej *et al.* 1980) as well as the growth of mycorrhizal fungi (Thompson and Medve 1984, Entry *et al.* 1987). It is not clear how soil pH and Al influence host/*Armillaria* relationships.

This study was initiated to determine: (1) relationships between soil extractable Al and pH and the incidence of Armillaria root rot in Douglas-fir plantations in western Washington, (2) the effect

¹Present address: Weyerhaeuser Company, Centralia Research Facility, 505 N. Pearl St., Centralia, Washington 98531

TABLE 1. Location of study sites in western Washington, *Armillaria* root disease severity, stand age, elevation, soil pH and extractable Al.

Site No.	<i>Armillaria</i> severity ¹	Location from nearest town (distance in km-bearing)	Stand age (years)	Elevation (m)	pH	2N KCl extractable Al (μg/g)	Water extractable Al (μg/g)
1	High	Hoquiam (19-NW)	5	30	4.90	312	8.3
2	High	Hoquiam (18-NW)	20	30	4.85	321	3.4
3	High	Blyn (14-SW)	20	910	4.62	15	0.5
4	High	Blyn (10-SW)	25	660	4.46	4	1.1
5	High	Silver Creek (7-S)	15	250	4.26	5	7.5
6	High	Silver Creek (10-SW)	20	200	4.19	3	5.0
7	High	Silver Creek (9-S)	25	250	4.47	1	6.7
8	High	Lebam (6-SW)	35	210	5.02	577	20.1
9	High	North Bend (3-NW)	10	180	5.84	109	28.6
Average ² ± SE for pH and extractable Al.			20	302	4.73 ± 0.20 ^a	149 ± 69 ^a	9.0 ± 3.1 ^a
10	Low ³	Hoquiam (8-NE)	5	60	4.88	1075	37.8
11	Low ³	Hoquiam (10-NE)	20	90	4.30	1958	50.4
12	Low	Blyn (5-S)	15	270	4.77	6	1.6
13	Low	Blyn (6-S)	18	670	4.98	7	2.1
14	Low	Blyn (7-S)	22	550	3.77	27	0.9
15	Low	Silver Creek (8-SW)	10	150	4.20	1	10.3
16	Low	Silver Creek (15-SW)	15	100	3.81	36	18.4
17	Low	Silver Creek (12-S)	20	200	4.12	9	22.4
18	Low	Silver Creek (6-S)	20	300	4.29	19	23.1
19	Low	Silver Creek (5-S)	25	200	4.51	20	9.3
20	Low	Raymond (6-E)	10	60	4.54	4	31.8
21	Low	South Bend (9-W)	10	60	4.97	271	21.3
22	Low ³	South Bend (9-W)	10	50	4.87	632	62.6
Average ± SE for pH and extractable Al.			15	212	4.46 ± 0.10 ^a	313 ± 164 ^a	22.4 ± 5.3 ^b

¹High severity (13-15 infected trees/ha); low severity (0-12 infected trees/ha).

²Averages followed by a different letter in the same column are significantly different (p < 0.05).

³No *Armillaria* root rot in these stands.

of soil extracts on growth of *Armillaria* in culture, and (3) the influence of Al and pH on *Armillaria* growth in culture.

Materials and Methods

Study Sites

Twenty-two Douglas-fir stands in western Washington were selected (Table 1). Sites 1-9 had high *Armillaria* severity (13-25 diseased trees/ha) while sites 10-22 had low disease incidence (0-12 diseased trees/ha). All stands were plantations except site 8. Stand ages varied from 5 to 35 years, averaging 20 years in high severity sites and 15 years in low severity sites (Table 1). Young stands were selected since *Armillaria* is less of a problem in older Douglas-fir stands (Hadfield *et al.* 1986). The stands were located in the coast range except site 9 which was located in the foothills of the Cascade

Mountains. Elevations ranged from 30 to 910 m with similar average elevations in high (302 m) and low (212 m) severity sites (Table 1).

Soil Chemistry

Soil samples were taken from three random locations at each of the 22 sites. At each location five systematic samples were taken from the top 5 cm of mineral soil, bulked and transported to the laboratory for analysis of extractable Al and pH. The top 5 cm was sampled because many of the roots and microbial activity are found in this zone. Rhizomorphs also commonly occur near the soil surface. Water extractable and 2N KCl extractable Al were determined using a modification of procedures by Barnhisel and Bertsch (1982). Two g of field soil were shaken in 200 ml of deionized water or 20 ml of 2N KCl for 4 hours and centrifuged. Solutions were analyzed on an IL 951

Atomic Absorption Spectrophotometer. Results were expressed as $\mu\text{g Al/g}$ oven dry soil (105°C). Soil pH was determined using a 1:1 (volume) soil distilled water mix and a pH meter (Fisher Accumet Model 210).

Source of *Armillaria* Isolates

Three diploid isolates of *Armillaria* were obtained from mycelium fans growing in infected but still living Douglas-fir trees in western Washington. Two isolates came from coastal sites near Hoquiam, while the third isolate was from a low elevation site in the Puget Sound area near Snohomish. All three diploid isolates were identified as *Armillaria ostryae* by cross plating using the method described in Guillaumin *et al.* (1991) with known testers provided by Dr. Duncan Morrison, Pacific Forestry Research Center, Victoria, British Columbia.

Armillaria Growth in Culture on Soil Extract Medium

The three *Armillaria* isolates were grown on unamended soil extract agar from Douglas-fir stands at Hoquiam (sites 1 and 11), Lebam (site 8), Raymond (site 20), and a fifth site near Snohomish, Washington, using technique M-26 outlined in Stevens (1974). Five replicate plates were used for each isolate and diameter growth was measured after 60 days of incubation at 20°C . Sixty days was used because of the very slow growth on the low nutrient soil extract medium. Some of the cultures developed rhizomorphs, but they were not included with the diameter measurements. Rhizomorph development tended to increase with decreasing pH. Fungal biomass is a better measure of growth than diameter because it includes rhizomorphs. Biomass was determined in a series of tests (Browning 1987). The linear correlation between biomass and diameter growth was positive ($r = 0.41$, $n = 90$) and significant ($p < 0.01$). Shaw (1985) also found that diameter and *Armillaria* dry weight were related in younger colonies. Thus it was felt that diameter growth correctly reflected growth trends even though rhizomorphs were not measured. Rhizomorphs are important in disease spread in the field.

Determination of Growth in Culture in Non-Buffered and Buffered Media

Non-Buffered Media. Isolates were grown in petri plates on 2% malt agar containing different

amounts of Al. $\text{AlCl}_3 \cdot 6\text{H}_2\text{O}$ salt was used as the source of Al^{3+} at concentrations of 0, 10, 25, 50, 100, and 200 mg Al/L. These concentrations were selected since they overlap the range of water extractable Al concentrations from the soil (0.5-62.6 $\mu\text{g/g}$) and fall in the range of 2N KCl extractable Al (1-1958 $\mu\text{g/g}$) (Table 1). The units $\mu\text{g Al/g}$ in soil and mg Al/L in solution are similar but not exactly equivalent because soil bulk density was not 1.0. Bulk densities typically ranged from 0.5 to 0.8 in these soils. Concentrations of Cl (0-788 mg/L) in the $\text{AlCl}_3 \cdot 6\text{H}_2\text{O}$ media are typical of those used in culture media (Stevens 1974, Robinson 1978) and should have had no influence on growth of *Armillaria*. The media were seeded with the three isolates on separate plates using a 5 mm cork borer and 5 replications of each treatment. Media pH was taken before autoclaving. Cultures were incubated at 20°C . Diameter growth of mycelium was measured in each plate after 30 days by averaging two perpendicular measurements.

Buffered Media. One percent malt extract media were buffered to pH 4, 5, and 6 by adding 0.1 M citric acid and 0.1 M trisodium citrate (McKenzie 1969). 1.0 N KOH and 1.0 N HCl were used to adjust the final pH. $\text{AlCl}_3 \cdot 6\text{H}_2\text{O}$ was added in concentrations of 0, 100, 200, and 300 mg Al/L. The media in petri plates were seeded with plugs of the three isolates using a 5 mm cork borer and 10 replications per treatment. Cultures were incubated at 20°C . Diameter growth of the mycelium was measured in each plate after 30 days by averaging two perpendicular measurements.

Statistical Analysis

Two-way analysis of variance was used to examine relationships among fungal growth, Al concentration and pH in buffered Al media at different pH levels. One-way analysis of variance was used to test growth differences among fungal isolates. A Newman-Keuls multiple-range test was used to determine significance. Regression analysis was used to examine relationships between soil pH and extractable Al concentrations, fungal growth and Al concentrations in soil extract media, and fungal growth and Al and pH in non-buffered and buffered media. Student t-tests were used to determine if means of soil pH, and water extractable and 2N KCl Al from high and low severity stands were different. The statistical package SYSTAT (Wilkinson 1989) was used on an Apple Macintosh IIfx computer.

Results and Discussion

Relationships Between *Armillaria* Incidence and pH and Al in the Field

It has been difficult to find strong relationships between expression of *Armillaria* root disease and field variables because many factors are involved, such as host vigor, abiotic stresses (light, temperature, moisture, nutrients, pH), presence or absence of inoculum, insects, other diseases, and management activities such as partial cutting (Wargo and Harrington 1991). Reaves *et al.* (1990) also suggested that burning may inhibit *Armillaria* by stimulating antagonistic fungi. We do not know the history of burning on our sites, however.

Armillaria is considered a disease of weakened trees (Wargo and Harrington 1991). Stress reduces host vigor and compromises host defenses. Aluminum toxicity to roots increases plant stress (Ulrich 1983) so it was hypothesized that Douglas-fir growing in soils in western Washington with the highest extractable Al concentrations would have the highest *Armillaria* root rot disease severity. However, the opposite situation was found. Sites with high disease severity had a significantly lower average water extractable Al concentration in the soil ($9.0 \pm 3.1 \mu\text{g Al/g}$) compared to sites with low severity ($22.4 \pm 5.3 \mu\text{g Al/g}$) (Table 1). No disease was observed on the sites with the highest water and 2N KCl extractable Al (Table 1).

It was expected that soils with the highest extractable Al concentrations would also be the most acidic since Al concentrations increase with decreasing pH (Ulrich 1983). However, there was not a significant relationship using regression analysis between soil pH and extractable Al in soils from the twenty-two sites. Soil pH and 2N KCl extractable levels were not significantly different between high and low severity sites. 2N KCl extractable Al averaged $149 \pm 69 \mu\text{g/g}$ in low severity sites and $313 \pm 164 \mu\text{g/g}$ in high severity sites (Table 1). Soil pH averaged 4.73 ± 0.20 and 4.46 ± 0.10 in high and low severity sites, respectively (Table 1). Although Redfern (1978), Shields and Hobbs (1979) and Singh (1983) found that low pH favored higher disease development under field conditions, Redfern and Filip (1991) suggested that data relating disease severity and soil pH in the field are generally inconclusive.

Because the influence of soil Al and pH on *Armillaria* severity was not clear from the field data,

a series of laboratory experiments were undertaken to determine the influence of Al and pH on *Armillaria* growth in culture. This involved determination of growth on soil extract media and non-buffered and buffered media containing various concentrations of Al at different pH levels.

Armillaria Growth on Soil Extract Media

Average diameter growth of the three *Armillaria* isolates in culture on five soil extract agars is shown in Figure 1 in relation to water extractable Al concentrations from these soils. There were no significant differences in growth among the three isolates so pooled data were used. *Armillaria* diameter growth tended to decrease with increasing soil water extractable Al concentrations (Figure 1). The logarithmic regression ($r = -0.86$, $n = 5$) is significant at $p < 0.05$, but the linear regression is not ($r = -0.74$). Growth data of this type are commonly not linear. Correlations between *Armillaria* diameter growth and 2N KCl extractable Al and pH were not significant. These data tentatively support the data in Table 1 which show that soils with higher average extractable Al have lower disease incidence, while pH was not significant.

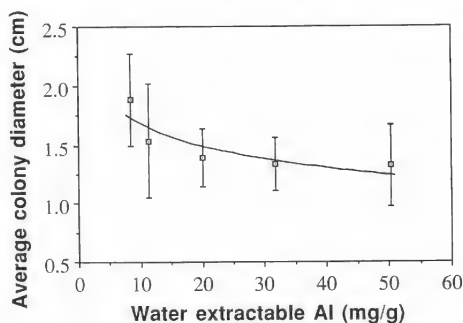


Figure 1. Average colony diameter after 60 days of three *Armillaria ostoyae* isolates from western Washington grown on soil extract agar in relation to water extractable Al from those soils. Standard errors and logarithmic regression line ($r = -0.86$, $n = 5$, $p < 0.05$) are shown. The linear regression was not significant ($r = -0.74$, $n = 5$)

Armillaria Growth on Non-buffered and Buffered Media

In order to separate the effects of Al and pH on *Armillaria* growth in vitro, the three isolates were grown on both non-buffered and buffered media.

Again there were no significant differences in growth among the three isolates so pooled data were used. In the non-buffered Al media growth decreased with increasing Al (Figure 2). The correlation between fungal growth and media Al concentration was high ($r = -0.81$, $n = 90$, $p < 0.001$). These isolates of *Armillaria* appeared very sensitive to Al. Aluminum has been found by others to negatively influence the growth of fungi in culture (Firestone *et al.* 1983, Muchovej *et al.* 1980, Orellana *et al.* 1975, Thompson and Medve 1984). The independent effects of Al and pH, however, cannot be evaluated using an unbuffered medium since pH fell from 5.8 in the 0 mg Al/L treatment to 2.6 in the 200 mg Al/L treatment.

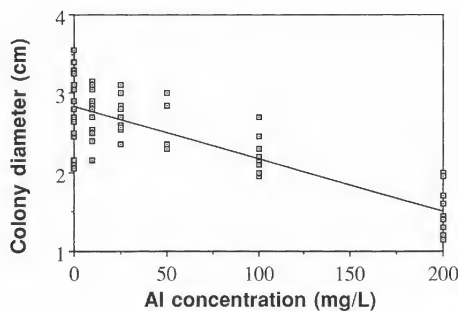


Figure 2. Colony diameter after 30 days of three *Armillaria ostoyae* isolates from western Washington in relation to Al concentration in non-buffered media. Media pH ranged from 2.8 (200 mg Al/L) to 6.0 (0 mg Al/L). $r = -0.81$, $n = 90$, $p < 0.001$ for linear regression line.

A buffered media was used to evaluate these independent effects. In buffered Al media at pH 4, growth of *A. ostoyae* decreased substantially with increasing Al (Figure 3A, $r = -0.84$, $n = 120$, $p < 0.005$). At pH 5 and 6 growth decline was less with increasing Al concentration (Figure 3B, $r = -0.41$, $n = 120$, $p < 0.01$ and Figure 3C, $r = -0.30$, $n = 119$, $p < 0.01$). Thus, growth seemed to be more affected by Al at pH 4 than at pH 5 or 6. A two-way ANOVA showed Al, pH, and the interaction between pH and Al to be significant. In nutrient solution studies of plants, it is well-documented that raising the pH generally relieves Al toxicity (Parker *et al.* 1988). It is unclear whether this is due to decreased solubility of Al^{3+} at higher pH, formation of non-toxic complexes, or a physiological response whereby low pH

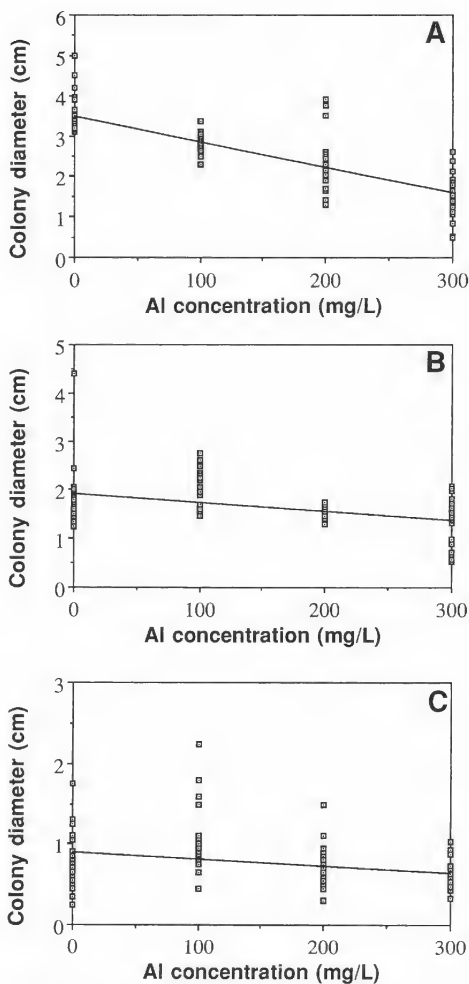


Figure 3. Colony diameter after 30 days of three *Armillaria ostoyae* isolates from western Washington in relation to Al concentration in buffered media at (A) pH 4, $r = -0.84$, $n = 120$, $p < 0.005$, (B) pH 5, $r = -0.41$, $n = 120$, $p < 0.01$ and (C) pH 6, $r = -0.30$, $n = 119$, $p < 0.01$.

predisposes the plant to Al injury (Parker *et al.* 1988). What mechanism is involved with *Armillaria* is unknown.

Armillaria growth in culture was strongly influenced by media pH in the absence of Al. Colony diameter increased with decreasing pH (Figure 4) ($r = -0.92$, $n = 90$, $p < 0.001$). The highest rate

of growth was observed at pH 4. Morrison (1974) found that the effect of pH on *Armillaria* growth varied with the fungal isolate; some isolates grew best on acidic media while others grew best on alkaline media. Further work by Morrison reported by Redfern and Filip (1991) suggested that these differences were actually related to species. *Armillaria ostoyae* and *A. mellea* grew better in acidic soil whereas *A. gallica* was either unaffected by pH or favored by alkaline soil.

Douglas-fir Response to Al

Laboratory studies are helpful in examining responses of fungi to specific environmental fac-

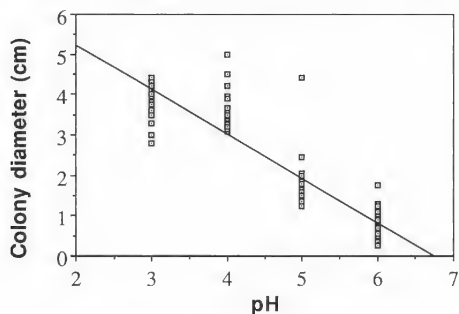


Figure 4. Colony diameter after 30 days of three *Armillaria ostoyae* isolates from western Washington in relation to pH in buffered media without Al. $r = -0.92$, $n = 90$, $p < 0.001$.

Literature Cited

- Anderson, J. B. 1986. Biological species of *Armillaria* in North America: redesignation of groups IV and VIII and enumeration of voucher strains for other groups. *Mycologia* 78:837-839.
- Barnhisel, R., and P. M. Bertch. 1982. Aluminum. In A. L. Page, R. H. Miller and D. D. Keeney (eds.). *Methods of Soil Analysis (Part 2). Chemical and Microbiological Properties*. Agronomy 9, 2nd ed. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin. Pp. 275-300.
- Browning, J. E. 1987. Influence of soil aluminum on *Armillaria* root disease in Washington State. University of Washington, Seattle, M.S. Thesis.
- Entry, J. A., K. Cromack, Jr., S. C. Stafford, and M. Castellano. 1987. The effect of pH on Al concentration on ectomycorrhizal formation in *Abies balsamiae*. *Can. J. For. Res.* 17:865-871.
- Firestone, M. K., K. Killham, and J. G. McColl. 1983. Fungal toxicity of mobilized soil aluminum and manganese. *Appl. Envir. Microbiol.* 46:758-761.
- tors, but they don't necessarily explain host response. Another factor to consider is host response to soil Al. Douglas-fir may not be as sensitive to Al as *Armillaria*. At pH 3.4 to 3.6, Douglas-fir seedling growth in solution culture was not negatively affected at concentrations as high as 4000 mg Al/L (Keltjens 1990), whereas *Armillaria* showed growth reductions at concentrations <300 mg Al/L at pH 4 (Figure 3A). Ryan *et al.* (1986a, 1986b) also found that Douglas-fir seedlings were relatively tolerant to high levels of Al. Furthermore, Keltjens (1990) suggested that in acidic forest soils with pH >4.0 and low Ca and Mg, moderate Al concentrations in the soil solution may play a beneficial role by alleviating the adverse effects of high H^+ concentrations in the soil solution. Organic acids in soil solutions can also ameliorate Al toxicity by complexing Al (Parker *et al.* 1988). The role of soil Al and pH in the Douglas-fir/*Armillaria* root rot relationship is not completely understood and needs further study.

Acknowledgments

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- Guillaumin, J. J., J. B. Anderson, and K. Korhonen. 1991. Life cycle, infertility, and biological species. In Shaw, C. G. Shaw III, and G. A. Kile (eds.). *Armillaria Root Disease*. USDA For. Serv., Agri. Handbook No. 691, Washington, D.C. Pp. 88-101.
- Hadfield, J. S., D. J. Coheen, G. M. Filip, C. L. Schmitt, and R. D. Harvey. 1986. Root diseases in Oregon and Washington conifers. USDA For. Serv., Pacific Northwest Region, Forest Pest Management, Portland, OR. R6-FPM-250-86.
- Hartley, C. 1928. Forest tree seedlings kept from damping-off by aluminum sulphate. *USDA Yearbook of Agriculture*. Pp. 332-334.
- Keltjens, W. G. 1990. Effects of aluminum on growth and nutrient status of Douglas-fir seedlings grown in culture solution. *Tree Physiol.* 6:165-175.
- Ko, W. H., and F. K. Hora. 1972. Identification of an Al ion as a soil fungitoxin. *Soil Sci.* 113:42-45.
- McDonald, G. I., N. E. Martin, and A. E. Harvey. 1987a. *Armillaria* in the northern Rockies. Pathogenicity and host susceptibility on pristine and disturbed sites. *USDA For. Serv., Res. Note INT 371*. Intermountain Res. Sta., Ogden, Utah. 5 p.

- _____. 1987b. Occurrence of *Armillaria* spp. of the Northern Rockies. USDA For. Serv., Res. Paper INT 381. Intermountain Res. Sta., Ogden, Utah. 7 p.
- McKenzie, H. A. 1969. pH and Buffers. In Dawson, R. M. C., W. H. Elhot, D. C. Elliot, and K. M. Jones (eds.). Data for Biochemical Research. 2nd ed. Oxford University Press, New York. Pp. 475-506.
- Morrison, D. J. 1974. Effect of soil pH on rhizomorph growth of *Armillaria mellea*. Canadian Forestry Service, Bi-Monthly Res. Notes 30:18-19.
- Morrison, D. J., D. Chu, and A. L. S. Johnson. 1985. Species of *Armillaria* in British Columbia. Can. J. Plant Path. 7:242-246.
- Muchovej, J. J., L. A. Maffia, and M. C. Muchovej. 1980. Effect of exchangeable soil aluminum and alkaline calcium salts on the pathogenicity and growth of *Phytophthora capsici* from green pepper. Phytopathology 70:1212-1214.
- Orellana, R. G., C. D. Foy, and A. L. Fleming. 1975. Effect of soluble aluminum on growth and pathogenicity of *Verticillium albo-atrum* and *Whetzelinia sclerotiorum* from sunflower. Phytopathology 65:202-205.
- Parker, D. R., T. B. Kinraide, and L. W. Zelazny. 1988. Aluminum speciation and phytotoxicity in dilute hydroxy-aluminum solutions. Soil Sci. Soc. Am. J. 52:438-444.
- Reaves, J. L., C. G. Shaw, II and J. E. Mayfield. 1990. The effects of *Trichoderma* spp. isolated from burned and non-burned forest soils on the growth and development of *Armillaria ostoyae* in culture. Northw. Sci. 64:39-44.
- Redfern, D. B. 1978. Infection by *Armillaria mellea* and some factors affecting host resistance and the severity of disease. Forestry 51:121-135.
- Redfern, D. B., and G. M. Filip. 1991. Inoculum and infection. In Shaw, C. G. Shaw III, and G. A. Kile (eds.). *Armillaria Root Disease*. USDA For. Serv., Agri. Handbook No. 691, Washington, D.C. Pp. 88-101.
- Robinson, P. M. 1978. *Practical fungal physiology*, John Wiley and Sons, New York.
- Ryan, P. J., S. P. Gessel, and R. J. Zasoski. 1986a. Acid tolerance of Pacific northwest conifers in solution culture: I. Effect of high aluminum concentration and solution acidity. Plant and Soil 96:239-257.
- _____. 1986b. Acid tolerance of Pacific northwest conifers in solution culture: II. Effect of varying aluminum concentration at constant pH. Plant and Soil 9:259-272.
- Shaw, C. G. III. 1985. In vitro response of different *Armillaria* taxa to gallic acid, tannic acid, and ethanol. Plant Pathol. 8:163-174.
- Shields, W. J., and S. D. Hobbs. 1979. Soil nutrient levels and pH associated with *Armillaria mellea* on conifers in northern Idaho. Can. J. For. Res. 9:45-48.
- Singh, P. 1983. *Armillaria* root rot: Influence of soil nutrients and pH on the susceptibility of conifer species to the disease. Eur. J. For. Pathol. 13:92-101.
- Stevens, R. B. 1974. *Mycology guidebook*. Univ. of Washington Press, Seattle.
- Thompson, G. W., and R. J. Medve. 1984. Effects of aluminum and manganese on the growth of ectomycorrhizal fungi. Appl. Environ. Microbiol. 48:556-560.
- Ulrich, B. 1983. Soil acidity and its relation to acid deposition. In B. Ulrich and J. Pankrath (eds.) *Effects of Accumulation of Air Pollutants in Forest Ecosystems*. D. Reidel Publishing Co., Dordrecht, Holland. Pp. 127-146.
- Wargo, P. M. 1980. *Armillaria mellea*: an opportunist. J. Arbor. 6:276-278.
- Wargo, P. M., and T. C. Harrington. 1991. Host stress and susceptibility. In Shaw, C. G. III, and G. A. Kile (eds.). *Armillaria Root Disease*. USDA For. Serv., Agri. Handbook No. 691, Washington, D.C. Pp. 88-101.
- Wargo, P. M., and C. G. Shaw. 1985. *Armillaria* root rot: The puzzle is being solved. Plant Dis. 69:826-832.
- Wilkinson, L. 1989. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.

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Bald Eagle Winter Roost Characteristics in Lava Beds National Monument, California

Abstract

This study provided a survey of bald eagle (*Haliaeetus leucocephalus*) winter roost habitat (in 4 km² of potential roost areas) in southern Lava Beds National Monument, California. A systematic-clustered sampling design ($n = 381$ plots) was used to compare forest stand characteristics in two primary roost areas (Caldwell Butte and Eagle Nest Butte) and two potential roost areas (Hidden Valley and Island Butte). A 100 percent inventory of roost trees in Caldwell Butte ($n = 103$ trees) and Eagle Nest Butte ($n = 44$ trees) showed they were spatially clumped and restricted to 12.7 percent and 2.8 percent, respectively, of the study areas. Roost trees, primarily ponderosa pine (*Pinus ponderosa*), averaged 81.1 ± 1.3 cm dbh (mean $\pm$ 1 S.E.) compared to non-roost trees (>35 cm dbh) that averaged 52.2 ± 1.0 cm dbh. Roost trees were generally taller and more open-structured than non-roost trees. All four study sites had adequate numbers of mid-sized trees (10 to 50 cm dbh) to replace the current stock of older, larger roost trees. However, seedlings and small trees (<10 cm dbh) in the roost areas were spatially clumped and few, suggesting that maintaining a continuous population of roost trees may be a problem in the distant future. Long-term studies of changing winter roost habitat and eagle use are essential to protect the bald eagle in the northwestern US.

Introduction

A critical stage in the population dynamics of the bald eagle (*Haliaeetus leucocephalus*) is the fall migration from areas of harsh to milder climates (Keister and Anthony 1983, USFWS 1986, Keister *et al.* 1987). The Klamath Basin of southern Oregon and northeastern California serves as one of the major winter roost areas in the lower 48 states (Keister 1981).

Wildlife biologists are becoming increasingly aware of the need to manage not only endangered species but also their habitat (Scott *et al.*, 1990, Hobbs and Hanley 1990). Bald eagle winter roost area characteristics in the northwestern US have been described as old-growth, multi-layered, forest stands (roost trees 100 to 535 years old) within 0.25 to 24 km of food resources (fish, carcasses, waterfowl in wetlands habitat, and various rodents in open forests) (Hansen *et al.* 1980, Keister 1981, Anthony *et al.* 1982). Careful monitoring of bald eagle habitat is essential because the habitat can be affected by a variety of land use practices including old-growth logging (Keister and Anthony, 1983) and draining wetlands for agriculture (USFWS 1986), and catastrophes including persistent drought, wildfire, and pathogen outbreaks (Martin and Johnson 1979, Dale and Kliejunas 1987).

The threats listed above are a real and present danger to winter roost sites in or adjacent to Lava Beds National Monument (LBNM) in northeastern

California. Proposed logging of old-growth timber south of LBNM in the Modoc National Forest and on private lands and the threat of wildfire in LBNM prompted this evaluation of the status of bald eagle winter roost habitat and a survey of potential ("or replacement") roost areas.

Specific objectives of this study were to: (1) quantify the characteristics and spatial distribution of roost trees; (2) identify roost trees recently used by bald eagles; and (3) survey the forest for potential roost areas throughout the study area.

Study Area

The Caldwell/Cougar Roost is between Cougar and Caldwell Buttes near the southeastern boundary of LBNM (Fig. 1). Sogge and Sydoriak (1990) provide additional details on the primary and secondary roost areas that represent about 4 km² and 7 km², respectively, of LBNM. Forest vegetation in the area has been classified broadly as stands of mixed conifers: ponderosa pine, western juniper (*Juniperus occidentalis*), white fir (*Abies concolor*), Shasta red fir (*A. magnifica shastensis*), sugar pine (*P. lambertiana*), lodgepole pine (*P. contorta*), incense cedar (*Calocedrus decurrens*), and curl-leaved mountain mahogany (*Cercocarpus ledifolius*) (Erhard 1979). Except for some preliminary information from Keister (1981), little is known about the size or age structure of the stands, or of the spatial distribution of roost trees and potential roost trees within the stands. The understory is composed primarily of bitterbrush (*Purshia*

LAVA BEDS NATIONAL MONUMENT

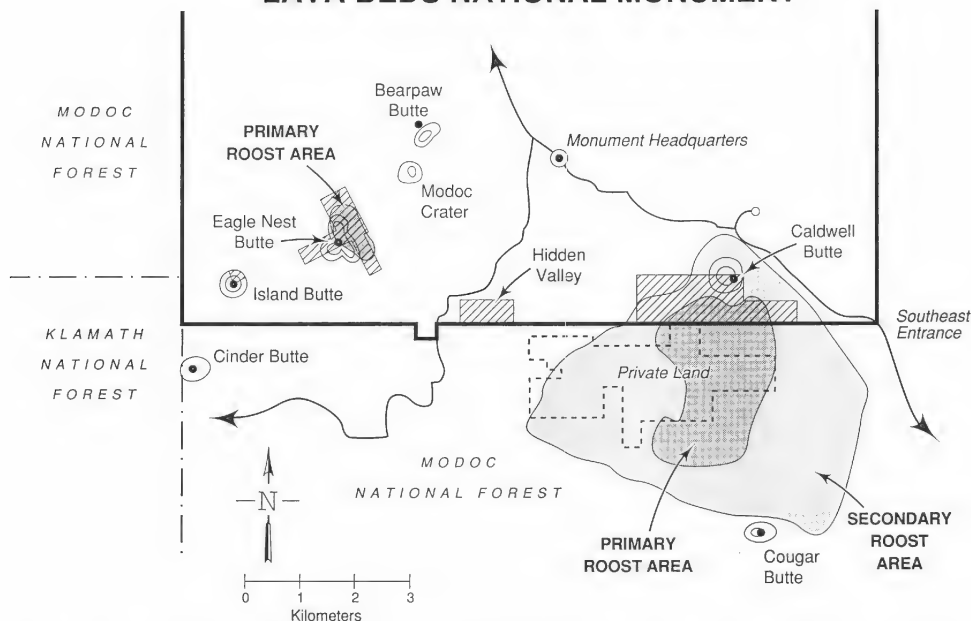


Figure 1. Map of Lava Beds National Monument (and adjacent lands), general locations of primary and secondary bald eagle winter roost areas (from Sogge and Sydoriak 1990), and study area locations (hatched areas).

tridentata), rabbitbrush (*Chrysothamnus* sp.), bitter cherry (*Prunus emarginata*), sagebrush (*Artemisia tridentata*), current (*Ribes* sp.), manzanita (*Arctostaphylos* sp.), and elderberry (*Sambucus* sp.) (Erhard 1979, Sogge and Sydoriak 1990).

The geology and physiography of the area are complex but little is known about their influences on forest development. The underlying volcanic substrate was formed within the last 1.25 million years, and some lava flows in the roost area are from the Holocene period (Donnelly-Nolan 1983). Glass mountain, south of the roost, erupted about 1,000 years ago, depositing frothy rhyolite pumice over the entire area (Chesterman 1955, Donnelly-Noland and Champion 1987).

Bald eagle use of the Caldwell/Cougar Roost Area varies annually. Maximum winter counts ranged from 360 eagles in January 1979 (Keister 1981) to 34 eagles in January 1990. Counts have decreased greatly since 1983/84 (278 eagles), with fewer than 60 eagles counted each year since then (Sogge and Sydoriak 1990). The reasons for this decrease are not understood at this time. Typically, bald eagles arrive in the area in November and

depart in February or March, with peak use in January (Sogge and Sydoriak 1990).

Previous studies have provided important baseline information on bald eagle winter roost characteristics in the general area. Krauss (1977) conducted a general survey of the Klamath Basin bald eagle winter use areas in 1976 and 1977. His observation suggested bald eagles in the Caldwell/Cougar roost area preferred tall, open-canopied ponderosa pines for roosting, but that eagles occasionally used tall snags and full canopy trees.

Keister (1981) compared general stand characteristics of five roost areas in the Klamath Basin with the point-quarter method (Mueller-Dombois and Ellenberg 1974). He found considerable differences between the Caldwell and Cougar roost stands in density (25.6 vs. 44.3 trees/ha) and number of stumps (0.3 vs. 12.2 stumps/ha), but similar mean tree diameters (50.4 vs. 56.0 cm dbh), tree heights (24.6 vs. 27.6 m) and "structure" classes. However, detailed information on the distribution of tree size classes was not reported, thus, it is impossible to fully assess spatial patterns or

potential vulnerability of the forest structure. For example, if all the old, tall trees are in one small area of the roost, one localized wildfire could greatly affect much of the habitat.

DellaSala *et al.* (1987) conducted a systematic survey of forest structure of the Bear Valley roost area in Oregon. A careful study design examined characteristics of individual roost trees and several forest structure attributes surrounding roost trees. A similar approach will be taken in this study.

Methods

Field surveys were conducted in two primary roost areas (Caldwell Butte and Eagle Nest Butte) previously identified by Sogge and Sydoriak (1990), and two potential roost areas in LBNM (Hidden Valley and Island Butte) known to have old trees. The size and shape of the study units were selected to encompass most of the preferred habitat in the area in the southern areas of the monument (Fig. 1).

Within each study unit, variable-radius circular plots were located in a systematic-cluster design (Legendre and Fortin 1989) with primary plots regularly located 150 m (by pacing) apart along west-east transects with secondary "cluster" plots located 60 m north-east of each primary plot. Because Eagle Nest Butte was a smaller, cliff-confined area, primary plots were located 75 m apart. The systematic-clustering sampling design has proven more efficient and effective in describing landscape features than straight systematic or random sampling designs (Legendre and Fortin 1989, Fortin *et al.* 1989). Vegetation plots had a radius of 12.6 m (0.05 ha) for trees ≤ 35 cm dbh, and a radius of 17.6 m (0.1 ha) for larger trees.

The origin (SW corner) of each grid was permanently marked (steel post) and given a letter, and distance and direction was measured to a bench mark or relocatable permanent feature of the landscape. Each plot was individually numbered (i.e., sampling unit and x,y coordinates in meters from the sampling unit origin). Physical information recorded at each plot included slope (%), aspect (e.g., N, NW, NE, etc.), and elevation (by altimeter to ± 10 m). An ocular estimate of percent shrub cover, herb cover, and grass cover was assigned to each 0.1-ha plot for general descriptive purposes.

Other vegetation characteristics were measured following methods in DellaSala *et al.* (1987) to allow comparison with other eagle roost areas. Within

a 12.6-m radius of each plot center (0.05 ha) trees ≤ 35 cm were tallied by species in four broad size classes ($>0-4$, 5-15, 16-25, 26-35 cm dbh).

Trees >35 cm dbh within a 17.6 m radius of the plot center (0.1 ha) were individually measured (dbh in cm) and assigned a species code, height class, structure class and castings class. Classes for tree heights, canopy structure and number of castings (i.e., regurgitated remains of eagle prey) followed DellaSala *et al.* (1987). Height classes were <10 , 11 to 20, 21 to 30, and >30 m. Casting classes (i.e., number of individual castings) were 0, 1 to 5, 6 to 11, 12 to 20, and >20 castings. Structure classes (Figure 2) were based on the tree canopy and crown classification system of Keen (1943) as modified by Keister and Anthony (1983). As in other bald eagle studies, castings found at the base of trees provided an index of habitat use (Keister 1981, DellaSala *et al.* 1987). Obvious roost trees ≤ 35 cm dbh (previously tagged trees or trees with castings) were individually recorded throughout each study area. Roost tree data included x,y coordinates and tree characteristics as defined above.

Site descriptions and forest structure were summarized for each study area (Caldwell Butte, Hidden Valley, Eagle Nest Butte and Island Butte). Emphasis was placed on the density, basal area, and spatial distribution of ponderosa pine (the preferred roost tree species).

Ponderosa pine roost trees and non-roost trees (>35 cm dbh) were compared for differences in mean diameter, percent trees by height class, and percent trees by structure class. The Students *t*-test was used to test for significant differences between roost tree and non-roost tree diameter using log-transformed data. For the Caldwell Butte and Eagle Nest Butte roost areas, spatial "contour" maps (SAS 1988) were used to display isolines of ponderosa pine density (by size class) and total basal area. The spatial distribution of known eagle roost trees is also presented.

Results

The number of plots and size of area sampled ranged from 214 plots in 2.4 km² in the Caldwell Butte area to 8 plots and 0.04 km² in the Island Butte area (Table 1). Current eagle roost areas (Caldwell and Eagle Nest Buttes) tended to be lower in elevation and have moderate slope values

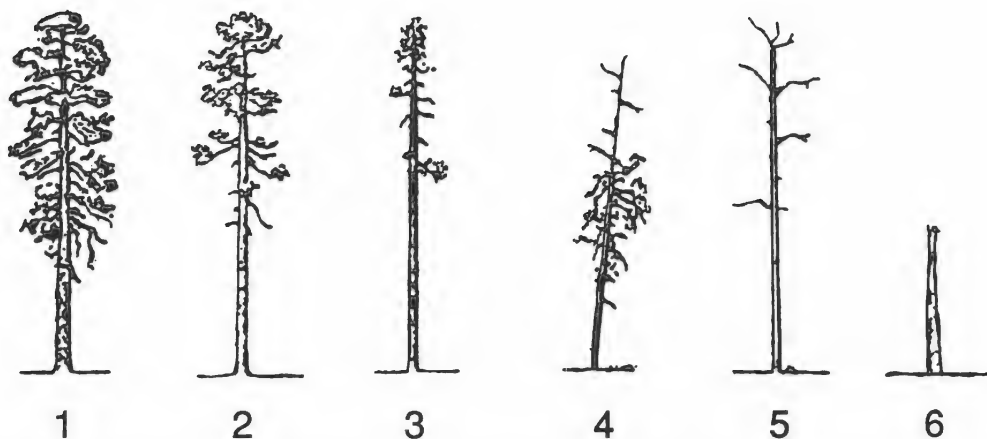


Figure 2. Characteristics used to classify tree structure within Lava Beds National Monument (adapted from Keen 1943, and Keister and Anthony 1983).

TABLE 1. Site characteristics of sampled bald eagle roost areas in Lava Beds National Monument.

Site Characteristics	Caldwell Butte	Eagle Nest Butte	Hidden Valley	Island Butte
Number of plots	214	108	51	8
Area Sampled (km ²)	2.4	1.2	0.4	0.04
Mean Elevation (m)	1440	1570	1580	1640
Aspect Range	1365-1634	1524-1667	1554-1597	1615-1670
Mean Slope (%)	14	16	7	26
(S.E.)	(1)	(2)	(2)	(2)
range	0-50	1-45	1-80	15-35
Mean Shrub Cover (%)	17	25	17	21
(S.E.)	(1)	(2)	(2)	(6)
Mean Herb Cover (%)	12	8	9	4
(S.E.)	(1)	(1)	(2)	(1)
Mean Grass Cover (%)	21	7	9	3
(S.E.)	(2)	(1)	(2)	(1)
Aspect of Plots %				
W	3.3	14.8	0	0
SW	3.3	0.0	2.0	0
SE	10.3	3.7	5.9	0
S	10.3	1.8	9.8	0
NW	13.8	13.9	17.6	0
NE	11.7	14.8	5.9	75
N	21.0	22.2	43.1	25
E	23.4	29.6	17.6	0

compared to non-roost areas (Hidden Valley and Island Butte). The four study areas were dominated by generally northern exposed plots and did not greatly differ in mean shrub, herb, or grass cover (Table 1).

Stand characteristics varied among the four study areas (Table 2). However, for ponderosa

pinus, and for the other species combined, the density of trees in the small to middle size classes (< 4, 5-15, 16-25 cm dbh) greatly exceeded the density of seedlings and the density of large size class trees (16-25, 26-35, > 35 cm dbh). Ponderosa pine total density was not as great as the total density of the other tree species combined (i.e.,

TABLE 2. Stand characteristics of roost areas (Caldwell Butte, Eagle Nest Butte) and potential roost areas (Hidden Valley, Island Butte) in Lava Beds N.M. Mean values per ha shown with standard error in parentheses.

Stand Characteristics	Caldwell Butte	Eagle Nest Butte	Hidden Valley	Island Butte
Mean Density (No./ha)				
Ponderosa Pine				
Seedlings	3.4 (1.7)	5.0 (1.5)	3.1 (1.0)	0.0
<4 cm dbh	15.4 (6.0)	16.9 (3.9)	9.4 (3.0)	5.0 (0.0)
5-15 cm dbh	23.4 (5.8)	30.0 (5.8)	19.2 (3.9)	0.0
16-25 cm dbh	15.6 (2.6)	22.6 (4.3)	16.1 (4.3)	0.0
26-35 cm dbh	11.7 (10.9)	10.6 (2.8)	8.2 (2.0)	7.5 (3.8)
>35 cm dbh	7.8 (1.0)	8.5 (1.8)	7.8 (1.9)	33.8 (6.0)
Total	77.3 (11.0)	93.6 (12.7)	63.8 (9.8)	46.3 (8.2)
Other trees ¹ (No./ha)				
Seedlings	2.1 (0.6)	19.4 (3.4)	12.5 (3.4)	27.5 (14.6)
<4 cm dbh	40.2 (4.2)	122.0 (8.4)	96.1 (10.9)	40.0 (18.1)
5-15 cm dbh	34.9 (3.7)	73.5 (5.8)	64.7 (9.0)	67.5 (21.4)
16-25 cm dbh	6.4 (1.3)	10.2 (1.6)	7.8 (2.9)	22.5 (7.0)
26-35 cm dbh	1.1 (0.4)	3.3 (1.0)	2.0 (0.8)	15.0 (6.3)
>35 cm dbh	7.3 (1.1)	21.5 (1.7)	0.0	28.8 (5.1)
Total	92.0 (8.1)	149.9 (14.6)	183.1 (21.5)	201.3 (54.8)
Mean Basal Area (m ² /ha) of trees >35 cm dbh				
Ponderosa Pine	16.4 (0.2)	31.8 (0.8)	19.8 (0.5)	143.0 (26.2)
Western Juniper	0.7 (0.3)	0.9 (0.6)	0.0	1.4 (0.1)
White Fir	0.2 (0.2)	0.4 (0.4)	0.0	42.0 (22.7)
Mountain Mahogany	0.0	0.0	0.0	0.0
Incense Cedar	0.1 (0.1)	0.0	0.0	0.0
Total	17.4 (0.2)	33.1 (0.8)	19.8 (0.5)	186.4 (29.0)

¹Includes species listed under basal area except ponderosa pine.

Western juniper, white fir, mountain mahogany and incense cedar). However, ponderosa pine accounted for between 76.7 percent and 100 percent of the basal area in the four areas. Thus, the dominant tree species and largest trees in the areas are ponderosa pines.

The absence of small ponderosa pine trees in the four areas is apparent in the size class distributions of the four areas (Figure 3). But, large trees (>50 cm) are also rare in the sub-populations of ponderosa pine (except for the clump of large trees sampled in the 200 m x 200 m Island Butte area).

The 2.4 km² Caldwell Butte study area contained 103 eagle roost trees compared to 44 eagle trees in the 1.2 km² Eagle Nest Butte area (Table 3). Only two of the 147 roost trees were not ponderosa pines: one white fir, one incense cedar. In both roost areas, roost trees were significantly larger in diameter than non-roost trees ($P < 0.05$, Students *t*-test on log-transformed data).

Most (89%) of the eagle roost trees were 21 to 30 m tall, while 77 percent of non-roost trees

were < 20 m tall. The majority (77.6%) of roost trees were open-structured, live trees. Snags were rarely used by bald eagles. Only 58 of 103 roost trees in the Caldwell Butte area had castings present, while 42 of 44 roost trees at Eagle Nest Butte were recently used (Table 3).

An analysis of the spatial distribution of ponderosa pine from the seedling stage to the eagle roost tree stage was conducted for Caldwell Butte (Figure 4) and Eagle Nest Butte (Figure 5). High density contour lines for seedling areas (i.e., >20 seedlings/ha) in the Caldwell Butte areas, for example, did not extensively overlap the current distribution of eagle trees (Figure 4). About half the 214 plots did not have pine seedlings. The low density contour lines for seedling areas (0 to 20 seedlings/ha) generally overlapped the high density isobars of the larger size class ponderosa pines. Thus, density information generated from the systematic clustering design used showed there are large portions of the study area without seedlings.

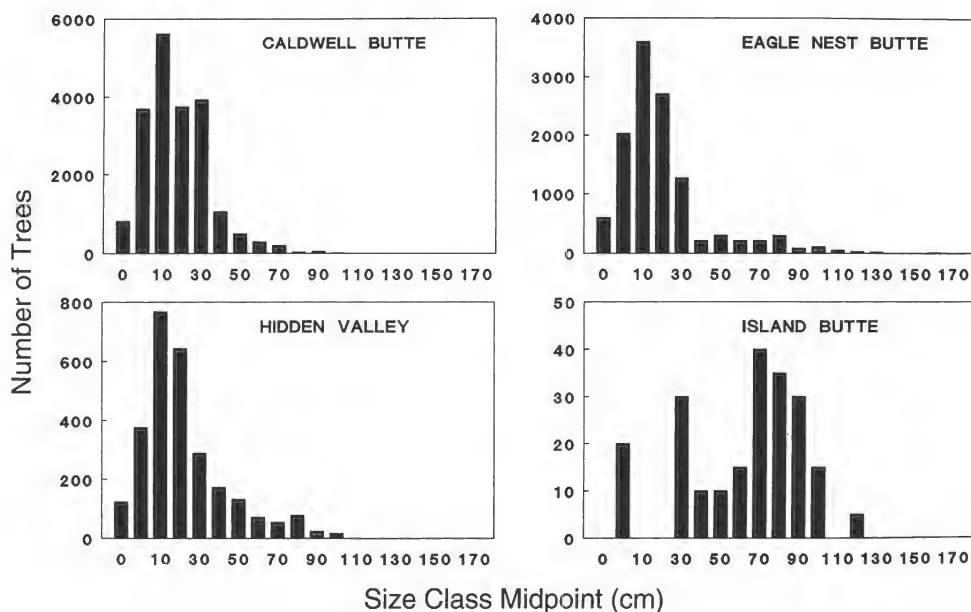


Figure 3. Size class distributions of ponderosa pines in roost areas (Caldwell Butte, Eagle Nest Butte) and potential roost areas (Hidden Valley, Island Butte).

TABLE 3. Characteristics of *Pinus ponderosa* (>35 cm dbh) by bald eagle roost area, Lava Beds National Monument, California.

Roost Area/ Tree Type	Number of Trees	Mean dbh cm ($\pm$ S.E.)	% trees by height (m)				% trees by structure class ¹						% trees by number castings			
			1-10	11-20	21-30	>30	1	2	3	4	5	6	0	1-5	6-11	12-20
Caldwell Butte																
Non-Roost	273	46.7 ² (1.0)	19.4	65.6	14.3	0.7	76.9	9.9	0.0	0.0	0.7	12.4				
Roost	103	80.3	1.0	8.7	90.3	0.0	21.4	73.8	1.0	0.0	2.9	1.0	43.7	42.7	8.7	4.9
Eagle Nest Butte																
Non-Roost	90	72.1 (1.8)	14.4	62.2	23.3	0.0	53.3	34.4	1.1	3.3	1.1	6.7				
Roost	44	83.0 (2.1)	0.0	11.4	88.6	0.0	2.3	93.2	0.0	2.3	2.3	0.0	4.6	77.3	9.1	9.1
Hidden Valley																
Non-Roost	70	51.3 ² (1.0)	10.0	61.4	28.6	0.0	80.0	12.9	0.0	2.9	1.4	2.9				
Island Butte																
Non-Roost	47	61.6 ² (1.0)	6.4	40.4	53.2	0.0	2.1	89.4	0.0	0.0	0.0	8.5				
All Roosts ³																
Non-Roost	480	52.2 ² (1.0)	15.8	61.9	21.9	0.4	65.6	22.7	0.2	1.0	0.8	9.6				
Roost	147	81.1 (1.3)	0.7	9.5	89.8	0.0	15.6	77.6	0.7	0.7	2.7	0.7	32.0	53.1	12.9	6.1

¹Structure class as adapted by Keister 1981 from Keen 1943. New structure class 6 contains broken snags.

²Averages based on log-transformed data.

³Averages weighted by numbers of trees.

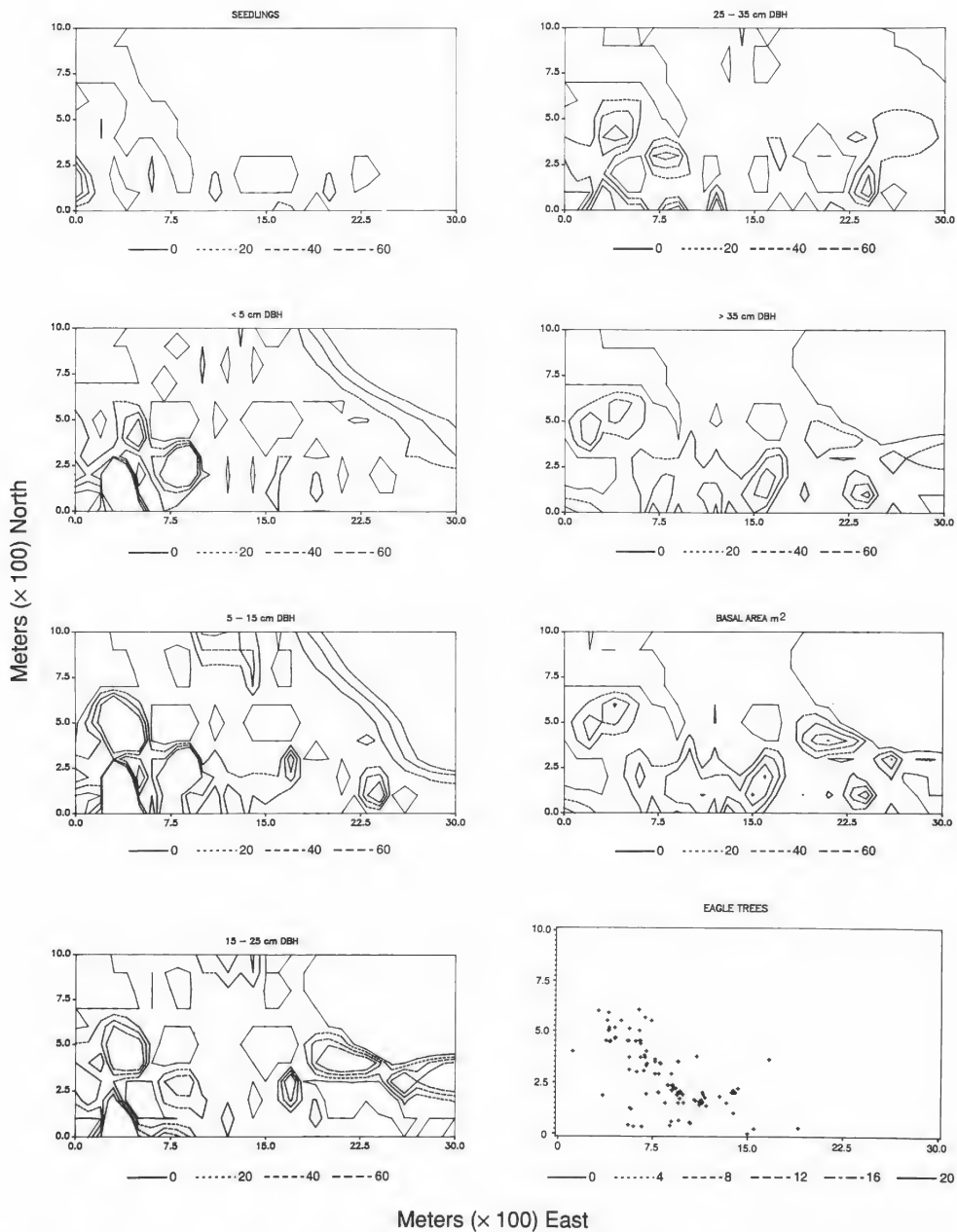


Figure 4. Density isobars (number of trees per ha) for different size classes of ponderosa pines, ponderosa pine basal area (m^2/ha), and spatial distribution of bald eagle roost trees in the Caldwell Butte study area.

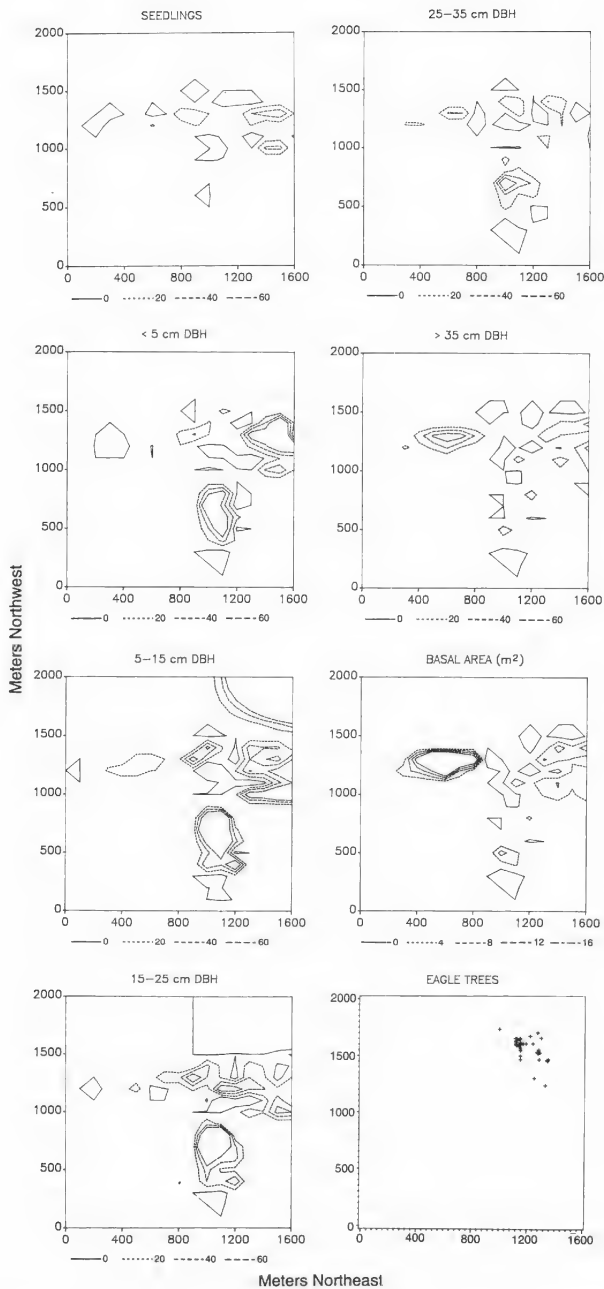


Figure 5. Density isobars (number of trees per ha) for different size classes of ponderosa pines, ponderosa pine basal area (m²/ha), and spatial distribution of bald eagle roost trees in the Eagle Nest Butte study area.

Likewise, high density contour lines of ponderosa pines >35 cm dbh and high contour lines of ponderosa pine basal area (m^2/ha), did not extensively overlap the current distribution of eagle trees (Figure 4). Areas of high pine basal area and large (>35 cm dbh) trees in the southwest corner of the Caldwell Butte area were not used by eagles.

Ponderosa pine seedlings and eagle roost trees were clumped in distribution in the Eagle Nest Butte area (Figure 5). The highest seedling density areas were adjacent to the eagle roost trees. Areas in the southeast portion of the roost area contain high densities of 0 to 35 cm dbh trees but no eagle roost trees. The areas of highest densities of >35 cm dbh ponderosa pines (and thus, areas of high basal area) in the southwestern portion of the study area also did not contain current eagle roost trees.

Calculations based on digitally recorded polygons of roost tree locations showed that 12.7 percent of the 2.4 km^2 Caldwell Butte study area and only 2.8 percent of the 1.2 km^2 Eagle Butte study area contained eagle roost trees. In each case, 3 outlying roost trees were excluded in the calculations of primary habitat.

Discussion

As shown in other studies in the Klamath Basin (Krauss 1977, Keister and Anthony 1983, DellaSala *et al.* 1987), bald eagle winter roost trees in LBNM tended to be more open-structured, larger (in diameter) and taller than non-roost trees (Table 3). However, it may be more important to examine differences, rather than similarities among winter roost areas to: (1) quantify relationships between habitat quality and eagle use; (2) identify the role of Caldwell Butte and Eagle Nest Butte in the local population dynamics of bald eagles; and (3) to evaluate better the management challenges that lie ahead.

Keister and Anthony (1983) showed the five major winter roost areas in the Klamath Basin greatly differed in area, number of roost trees, and number of castings found in 1979. Based on their census, less than 8 percent of the eagle use occurred in the Caldwell roost area. The concentration of eagle use I calculated at Caldwell was the lowest of the five areas with 8 castings/ha. Because eagle use in the five Klamath Basin roost areas was generally proportional to the number of available roost trees (Keister and Anthony 1983), the Caldwell Butte and Eagle Nest Butte areas may have

been (and may continue to be) low eagle use areas compared to the other roost areas in the Klamath Basin.

Because stand characteristics (i.e., species composition, size structure, age structure), distance to feeding grounds, and annual eagle use vary considerably among the roost areas in the Klamath Basin, it is not easy to assess or compare habitat quality of eagle roost areas. Within the Caldwell Butte and Eagle Nest Butte areas in LBNM, habitat quality was highly variable and spatially concentrated. For uncertain reasons, not all areas with large trees were used by eagles (Figures 4 and 5). Areas currently unused by the eagles may be more exposed to wind, have no traditional use, or have other resource limitations not yet identified in field studies. Alternatively, eagle populations may not be high enough to disperse into the currently unused areas.

For the same reasons, it is difficult to identify "potential" roost areas. The stand characteristics of Hidden Valley were generally intermediate between those of Caldwell Butte and Eagle Nest Butte (Tables 1 to 3, Figure 3). There are many large trees in the area with no sign of past eagle use. Furthermore, the gregarious nature of bald eagles during the winter roost period may discourage the "colonization" of potential roost areas by one or two adventurous individuals. Such dispersal/colonization events may occur only infrequently during peak population periods.

Continued bald eagle use in the Caldwell Butte and Eagle Nest Butte areas may be, in part, largely dependent on the population dynamics of ponderosa pines (i.e., the continued availability of large trees). There are many medium-sized trees in both study areas (Figure 3). And, many of these trees are located in specific areas currently used by bald eagles (Figures 4 and 5). Thus, barring major catastrophes (extreme fire or pathogen outbreaks, etc.) over the next 50 to 100 years, there should be an adequate number of replacement roost trees in the tree population. All four study areas, however, had very few small trees (Figure 3). Thus, there may be a discontinuous supply of large trees to the population in the long-term.

The population dynamics of ponderosa pine in LBNM appear temporally and spatially complex. Compared to similar-sized bald eagle roost trees elsewhere in the Klamath Basin (Keister 1981, DellaSala *et al.* 1987), roost trees in the Caldwell Butte roost area grow much more slowly and live

longer (mean age = 289 years) than trees in the Three Sisters, Mt. Dome, and Bear Valley roosts. Thus, the cycling of trees from the seedling stage to the roost tree stage may be much slower in the drier and more sparsely vegetated pine stands in LBNM. Very little information is available on the age structure of ponderosa pine stands in the area: no systematic survey has been undertaken. Thus, stage-class or age-class projections are problematic at this time.

The population dynamics of ponderosa pine in Caldwell Butte and Eagle Nest Butte also were spatially complex. Seedling distribution and eagle roost trees were spatially clumped and not necessarily overlapping other size class trees on the landscape (Figures 4 and 5). Two important factors influencing the size distribution and spatial patterns of ponderosa pines are insect outbreaks and fires. Western pine beetle (*Dendroctonus brevicomis*) infestations in the 1920's reportedly killed large numbers of large trees (Dale and Kliejunas 1987). However, lack of fires due to a full fire suppression policy from 1910 to 1974 (Sogge and Sydoriak 1990) may have severely limited pine reproduction.

Historically, lightning-caused fires in the Caldwell Butte area occurred on average 11 years apart (range 2 to 18 years; Olsen and Martin 1982). Most of these fires were small (<0.1 ha) and other than three small fires in 1970 and 1972, the natural role of fire has greatly diminished in these ecosystems (Martin and Johnson 1979, Olsen and Martin 1982, Sogge and Sydoriak 1990). An active prescribed burning program may be necessary to reduce heavy fuels and the possibility of catastrophic fires in currently used roost areas. This also will promote the establishment of pine seedlings that are scarce (Figure 3) and noticeably absent in many areas (Figures 4 and 5).

These findings confirm the many management challenges previously identified for the continued protection of bald eagle roost habitat in the Klamath Basin (Keister and Anthony 1983, DellaSala *et al.* 1987). The decrease in eagle use since 1983/84 probably warrants an intensive annual monitoring of eagle use.

A lack of ponderosa pine seedlings perhaps due to drought or to decades of fire suppression indi-

cates a need to enhance pine regeneration by prescribed burning selected areas. However, barring unforeseen catastrophes, the large number of medium-sized trees in the Caldwell Butte and Eagle Nest Butte areas should ensure that short-term habitat requirements are met.

Eagles have not expanded into similar nearby habitat (e.g., Hidden Valley, Island Butte) despite the presence of large open-structured trees. Thus, the current understanding of roost area characteristics and eagle behavior make it difficult to identify or assess potential or alternate roost sites. Logging in currently used bald eagle roost areas should be curtailed until we can accurately identify alternate roost sites that may be used annually by bald eagles.

Additional studies of bald eagle habitat characteristics, population dynamics of ponderosa pines, and bald eagle roost behavior are needed. These studies should be carried out on a state-wide or Klamath Basin-wide scale and over several years. They should be conducted in a hierarchical fashion (as suggested by DellaSala *et al.* 1987) at three spatial scales: tree level, plot level, and sub-roost or roost level. Winter roost activity should be carefully monitored at all roosts and sub-roosts. The systematic-clustering sampling design used in this study could easily be expanded to the other roost areas and areas of potential habitat. Because of the patchy nature of eagle trees on the landscape, a 100 percent inventory of roost trees is essential and should be repeated periodically in the future.

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- Anthony, R. G., R. L. Knight, G. T. Allen, B. R. McClelland, and J. I. Hodges. 1982. Habitat use by nesting and roosting bald eagles in the Pacific Northwest. *Trans. North. Amer. Wildl. Nat. Resour. Conf.* 47:332-342.
- Chesterman, C. W. 1955. Age of obsidian flow at Glass Mountain, Siskiyou County, California. *Amer. J. Science* 253:418-424.
- Dale, J. and J. K. Kleijunas. 1987. A biological evaluation of forest pest conditions at the Caldwell Butte eagle roost area, Lava Beds National Monument. U.S. Forest Service, Pacific Southwest Region. Forest Pest Management Report No. 87-9.
- DellaSala, D. A., R. G. Anthony and T. A. Spies. 1987. A habitat management plan for bald eagles (*Haliaeetus leucocephalus*) communal roost sites at the Bear Valley National Wildlife Refuge, Oregon. Report to U.S. Fish and Wildlife Service, Klamath Basin National Wildlife Refuge, Contract No. 14-16-0009-1533. RWO #7.
- Donnelly-Nolan, J. M. 1983. Structural trends and geothermal potential at Medicine Lake Volcano, Northern California. *EOS Transactions, Amer. Geophys. Union* 64:898.
- Donnelly-Nolan, J. M. and P. E. Champion. 1987. Geologic map of Lava Beds National Monument, Northern California. U.S.G.S. Map 1-1804.
- Erhard, D. H. 1979. Plant communities and habitat types in the Lava Beds National Monument, California. M.S. Thesis. Oregon State University, Corvallis, Oregon.
- Fortin, M. J., P. Drapeau and P. Legendre. 1989. Spatial autocorrelation and sampling design in plant ecology. *Vegetatio* 83:209-222.
- Hansen, A. J., M. V. Stalmaster, and J. R. Newman. 1980. Habitat characteristics, function, and destruction of bald eagle communal roosts in western Washington. *In* R. L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen, eds. *Proceedings Washington Bald Eagle Symposium*, Seattle. Pp. 221-230.
- Hobbs, N. T. and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? *J. Wildl. Manage.* 54:515-522.
- Keen, F. P. 1943. Ponderosa pine tree classes redefined. *J. For.* 41:249-253.
- Keister, G. P., Jr. 1981. Characteristics of winter roosts and population of bald eagles in the Klamath Basin. M.S. thesis. Oregon State University, Corvallis, OR. 82 pp.
- Keister, G. P., Jr. and R. G. Anthony. 1983. Characteristics of bald eagle communal roosts in the Klamath Basin, Oregon and California. *J. Wildl. Manage.* 47:1072-1079.
- Keister, G. P., Jr., R. G. Anthony and E. J. O'Neill. 1987. Use of communal roosts and foraging areas by bald eagles wintering in the Klamath Basin. *J. Wildl. Manage.* 51:415-420.
- Krauss, G. D. 1977. A report on the 1976-1977 Klamath Basin bald eagle winter use area investigation. USDA Forest Service, Klamath National Forest. 68 pp.
- Legendre, P. and M. J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetation* 80:107-138.
- Lehman, R. N. 1988. Mount Dome habitat management plan. USDI Bureau of Land Management, Susanville District, CA. 81 pp.
- Martin, R. E., and A. H. Johnson. 1979. Fire management of Lava Beds National Monument. *In* Linn, R. M. (ed.) *Proceedings of the First Conference on Scientific Research in the National Parks*. Vol. II. National Park Service and American Institute of Biological Sciences, Washington, D.C. Pp. 1209-1218.
- Mueller-Dombois, D. and H. Ellenberg. 1974. *Aims and methods of vegetation ecology*. John Wiley and Sons. New York, NY. 547 pp.
- Olsen, C. and R. E. Martin. 1982. Recommended program for fire management at Lava Beds National Monument, California. N.P.S. Western Region Final Report, Contract CX-8000-9-0015.
- SAS. 1988. SAS for Personal Computer. Release 6.03 edition. SAS Institute, Inc. Cary, NC.
- Scott, M. J., B. Csuti, K. Smith, J. E. Estes and S. Caicco. 1990. Beyond endangered species: an integrated conservation strategy for the preservation of biological diversity. *Endangered Species UPDATE* 5(10):43-48.
- Sogge, M. and C. Sydoriak. 1990. Caldwell/Cougar bald eagle winter roost management plan. Lava Beds National Monument and Modoc National Forest, CA. 32 pp.
- U.S. Fish and Wildlife Service. 1986. Pacific bald eagle recovery plan. USDI. Portland, OR. 163 pp.

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Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1990).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

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May 1993

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MEETING ABSTRACTS



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Program and Abstracts

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March 24-27, 1993

Eastern Oregon State College, La Grande, Oregon

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Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

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Announcements

Outstanding Scientist Award

Dr. Wayne Minshall was honored as Outstanding Scientist at the 66th Annual Meeting of the Northwest Scientific Association, March 24-27 at Eastern Oregon State College in La Grande. Dr. Minshall has been Professor of Ecology in the Department of Biological Sciences at Idaho State University since 1966. He has a B.S. degree in fisheries management from Montana State University (1961) and a Ph.D. in zoology from the University of Louisville (1965).

Minshall, an internationally recognized expert on the ecology of flowing waters, is regarded as one of the foremost stream ecologists in the world. His research interests emphasize aquatic benthic invertebrates, community dynamics, stream ecosystem structure and function, and stream habitat and biotic assessment. For the past 10 years, he has been conducting research on the effects of wildfires and other disturbances on stream ecosystems, including the recovery of Yellowstone National Park streams following the 1988 fires.

Minshall has authored over 70 peer-reviewed journal articles and 40 technical reports. He is co-editor with J. R. Barnes of *Stream Ecology: Application and Testing of General Ecological Theory*, and has co-authored several books on stream/riparian habitat. Twenty Master's students and 12 Ph.D. students have completed their programs under his direction.

He has received over 65 research grants and contracts totaling more than \$2.8 million from a variety of sources, including the National Science Foundation, USDA Forest Service, U.S. Soil Conservation Service, National Park Service, The Nature Conservancy, and the Smithsonian Institution.

Minshall was named the 1988 Idaho State University Distinguished Researcher, and was one of the 100 Idahoans profiled in the Idaho Centennial commemorative book *Here We Have Idaho: People Make a Difference* published in 1990. Dr. Minshall certainly *has* made a difference as a scientist in the Pacific Northwest, and we congratulate him as Outstanding Scientist.



Lifetime Membership Award

Dr. Ken Kardong was also honored at the 66th Annual Meeting of the Northwest Scientific Association. He was presented with a Lifetime Membership Award for his service to the association as Editor of *Northwest Science*. During his six years as Editor, Dr. Kardong was widely recognized for his professionalism and dedication to the scientific quality of the journal. He handled approximately 200 manuscripts from a wide diversity of disciplines, and was well-respected for his ability to work with authors and associate editors to review, revise, and publish first-rate manuscripts.

Since stepping down as Editor, Dr. Kardong has continued with his duties as Professor of Zoology at Washington State University, albeit with a little more time. The Lifetime Membership Award is a small token of our appreciation for his outstanding work as Editor of *Northwest Science*.

Habits of Bald Eagles Wintering along the Crooked River, Oregon

Abstract

Bald eagles (*Haliaeetus leucocephalus*) were observed in the upper Crooked River drainage in central Oregon from January to April, 1986 and 1987 to locate roosts and to describe roosting habitat, eagle abundance, and foraging behavior. The number of eagles peaked at ≈ 115 during the weeks of 10 March 1986 and 2 March 1987. Large mammal carcasses (deer and cattle) were the primary food source for eagles during January and February. Ground squirrels (*Spermophilus* spp.) were important food during March and April. Twelve communal night roosts were generally in the largest trees in the vicinity of feeding areas and were isolated from human activities. All roost trees but one cottonwood (*Populus deltoides*) were conifers and were the dominant, open-structured individuals in forest stands. Results indicate that: 1) substantially more bald eagles (100+) utilize eastern Oregon in winter than was previously thought, 2) use of large mammal carrion by bald eagles can be enhanced by not placing carcasses in pits, opening intact carcasses to expose flesh and viscera, and placing carcasses at least 250 m from human activities, and 3) large (63-152 cm diameter at breast height) coniferous trees that are near feeding areas and isolated from human activities are chosen for communal night roosting. Management of bald eagle roosting habitat should include maintenance of stands of large coniferous roost trees, planting of deciduous trees with horizontal limb structure (e.g., cottonwood) near feeding areas, and protection of riparian zones from livestock grazing.

Introduction

Bald eagles often roost communally near abundant sources of food during winter. In the Pacific Northwest, waterfowl concentrations (Keister *et al.* 1987, Isaacs and Anthony 1987) and spawning salmon (McClelland *et al.* 1982, Stalmaster *et al.* 1979) attract large numbers of bald eagles, and communal night roosts are common in these areas. The reason for communal roosting is poorly understood (Anthony *et al.* 1982, Keister *et al.* 1985). One function may be for communicating locations of food (Ward and Zahavi 1973).

Peak counts of 32-55 bald eagles, primarily foraging on large mammal carrion, were reported along the Crooked River in central Oregon during winter, 1978-1984 (U.S. Bur. Land Manage., unpubl. data), but only one roost was located (R. Hickenbottom, U.S.D.A. For. Serv., pers. comm.). Because of the threatened status of the species (U.S. Dept. Inter. 1978), concerns were raised about the possible effects of timber management on unknown communal roosts along the Crooked River. As a result, we studied the habits of bald eagles wintering along the Crooked River, Crook Co., Oregon during the winters of 1986 and 1987. Our

objectives were to locate roosts and describe roosting habitat, eagle abundance, and foraging behavior.

Study Area

The study area, located in central Oregon, included the Crooked River drainage from Prineville Reservoir east (upstream) to Rager Ranger Station (Figure 1). The Crooked River, above Prineville Reservoir, drains the Ochoco Mountains to the north, the Blue Mountains to the east and south-east, and the Maury Mountains to the south. Elevations range from 986 m at Prineville Reservoir to 2111 m at Lookout Mountain in the Ochoco Mountains. The climate is semi-arid with low annual precipitation (mean = 30 cm), low humidity, and a wide range between daily maximum and minimum temperatures (Franklin and Dyrness 1973).

Most of the floodplain of the Crooked River and its major tributaries is privately owned and has been converted to pastureland. Individual or small groups of deciduous trees are scattered in the river valley. Natural vegetation zones vary by elevation and aspect; dominant species in order of increasing elevation are juniper (*Juniperus occidentalis*), ponderosa pine (*Pinus ponderosa*), and grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) (Franklin and Dyrness 1973).

¹Current address: Oregon Department of Fish and Wildlife, 7118 NE Vandenberg, Corvallis, Oregon 97330

²Current address: U.S.D.A. Forest Service, 348855 Ochoco Ranger Station, Prineville, Oregon 97754

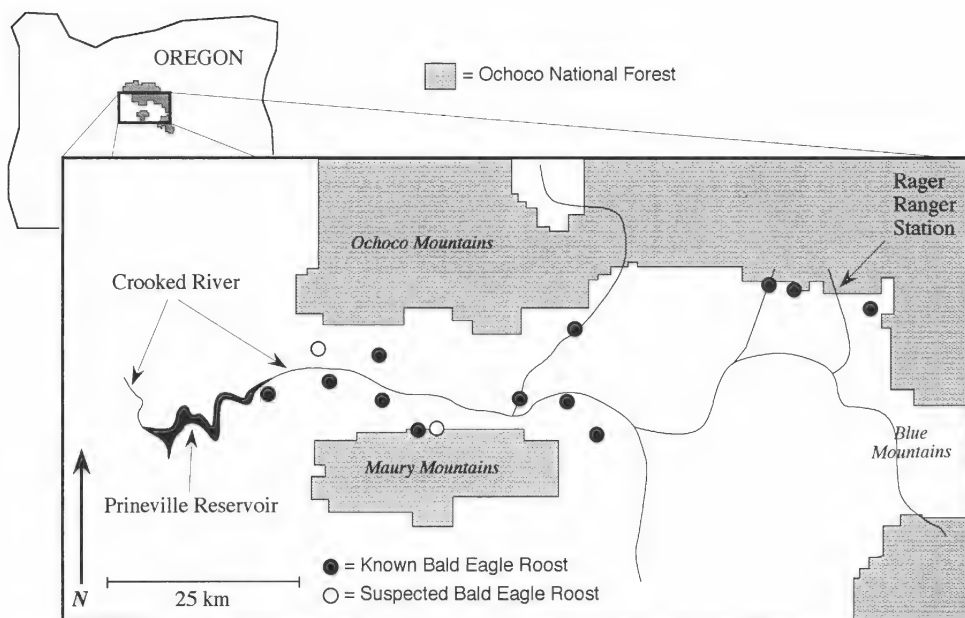


Figure 1. Map showing the study area for wintering bald eagles and locations of communal night roosts along the Crooked River in central Oregon, 1986-1987.

Methods

Counts of bald eagles were conducted weekly from January through April, 1986 and 1987, to estimate the bald eagle population and to determine principal feeding areas and foods. We began counts at 0900 h, after most eagles had left night roosts to feed, and tried to complete counts by 1300 h so that birds leaving the feeding areas to soar, loaf, or return to roosts were not missed. Counts were made by two parties of one or two people driving all-weather, public roads. Each party covered $\approx 1/2$ of the study area by driving slowly (16-64 km/h) in opposite directions from a starting point at Milepost 46 on Highway 380. We stopped at 0.4-3.2 km intervals to scan the surrounding area with binoculars and spotting scope and try to locate every eagle present. Age class (adult = all white head and tail, subadult = any degree of brown in head or tail feathers, or unknown = plumage not distinguishable), location, activity, and time were recorded for each eagle observed.

Aerial counts of eagles were conducted weekly from 27 February to 26 March 1986 at the same time as driving counts. Aerial counts were made

by a pilot and two observers, flying low (100-500 m) and slow (95-130 km/h) over the driving survey route in a Cessna 172 fixed-wing aircraft. Age class, location, activity, and time were recorded for each bald eagle observed. Air and ground counts were used to calculate a double-survey estimate of population size (Magnusson *et al.* 1978):

$$N = [(S_1 + B + 1)(S_2 + B + 1) / (B + 1)] - 1$$

where:

N = the population estimate

S_1 = bald eagles seen from the air but not from the ground

S_2 = bald eagles seen from the ground but not from the air

B = bald eagles seen by both surveys.

We used differences in counts of adults and subadults between survey types to calculate S_1 , S_2 , and B . For example, an air survey count of 21 adults + 9 subadults (30 eagles) and a ground survey count of 20 adults + 15 subadults (35 eagles) would yield an S_1 value of 1 [(21 - 20) + 0], an S_2 value of 6 [0 + (15 - 9)], and a B value of 29 (20 + 9); therefore, $N = [(1 + 29 + 1)(6 + 29 + 1) / (29 + 1)] - 1$ would result in a population estimate of 36 eagles.

Carcass surveys were conducted twice weekly during 1986 and once per week during 1987, by

one or two people driving the survey route. During those surveys we searched for new carcasses and observed bald eagle activity at previously located carcasses. Location, species, description (age class, size, and color), and condition (1 = apparently intact, no meat showing; 2 = open, meat showing but no part of the skeleton exposed; 3 = part of the skeleton exposed, >50% of the meat remaining; 4 = <50% of the meat remaining; 5 = stripped, apparently little or no meat remaining) were recorded for all mule deer (*Odocoileus hemionus*) and cattle carcasses. Condition was recorded only during the first observation of the carcass in 1986. In 1987, carcass condition was recorded during each observation. Age class, distance from carcass, and activity (feeding, flying, perching, flushing due to disturbance, etc.) of eagles within 500 m of carcasses were recorded during each observation. Additional carcass observations were made when counting eagles.

Flights of eagles leaving feeding areas during late afternoon were observed and mapped. If a consistent pattern of flights to a particular area was observed, that area was searched for a communal night roost. Once a roost was located, roost counts were conducted weekly, as long as eagles continued to use the roost. Eagles were counted leaving roosts at dawn or arriving at roosts at dusk. Age class, flight direction and altitude, and time were recorded for each bald eagle observed. During 1987, volunteers from local communities were organized to conduct weekly counts at previously-located roosts so that we could search for unknown roosts.

Trees >30.5 cm diameter at breast height (dbh) in communal roosts were measured during July 1986. The 30.5 cm dbh limit was selected because use of trees that size or smaller for roosting has not been reported for the Pacific Northwest (Anthony *et al.* 1982, Isaacs and Anthony 1987). Species, dbh, and height were recorded for all trees measured. Conifers were also given one of five structure classifications (1 = live top with no large dead lateral limbs, 2 = mostly live top with few large dead lateral limbs, 3 = mostly dead top with several large dead lateral limbs, 4 = dead top with large dead lateral limbs and some live lower limbs, 5 = completely dead with large dead lateral limbs) (Isaacs and Anthony 1987). A tree was considered a roost tree if there was one or more intact castings below the tree. Roost tree characteristics (species, dbh, height, and structure

class for conifers) were determined by measuring all roost trees. Roost stand characteristics (species, dbh, height, and structure class for conifers) were determined from a systematic sample of trees >30.5 cm dbh. Castings below all roost trees were counted and categorized by condition (intact or piece) and primary composition (i.e., fur or feathers).

Student's t-test statistic was used to test for differences between mean stand and roost tree characteristics. Chi-square goodness-of-fit tests and Bonferroni confidence intervals (Byers *et al.* 1984) were used to evaluate carcass use and eagle reaction to human activities.

Results and Discussion

Timing and Abundance

In 1986, the number of eagles seen during driving counts increased steadily from 23 during the week of 6 January to 86 during the week of 10 March (Figure 2), then dropped sharply to two eagles in the last week of April. In 1987, numbers of eagles stayed below 20 until the last week of January, when 46 were counted. Counts through February were similar to 1986. The peak count in 1987 occurred one week earlier (week of 2 March) than in 1986, and counts for the remainder of 1987 continued to be one week ahead of the 1986 pattern (Figure 2). Prior to 1986, numbers of bald eagles along the Crooked River increased

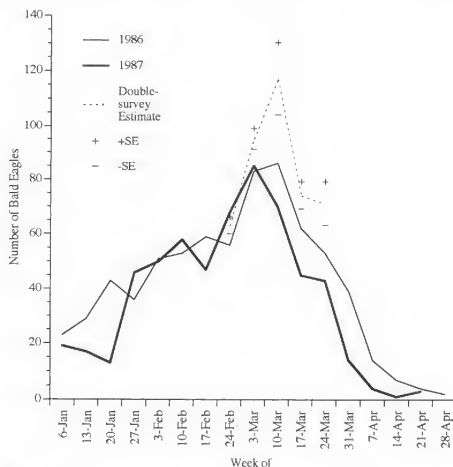


Figure 2. Weekly driving counts and double-survey estimates of bald eagles along the Crooked River, Oregon, 1986-1987.

through January and February, peaked in mid-February (1 year), March (4 years), and early-April (1 year), and declined through April and early-May (U.S. Bur. Land Manage., unpubl. data). Mean date of peak count for 1979-84, 1986 and 1987 was 13 March ($n = 8$, $SD = 17.4$ days).

Timing of peak abundance differed among years (U.S. Bur. Land Manage., unpubl. data, This study) and probably resulted from annual variations in and interactions among weather, food abundance, timing of bald eagle migration, and timing of counts. Variations in timing of peak abundance have been related to weather and food abundance in the Harney Basin of southeastern Oregon (Isaacs and Anthony 1987), the Klamath Basin of Oregon and California (Keister *et al.* 1987), and Glacier National Park, Montana (McClelland *et al.* 1982).

We observed a substantial increase in numbers of bald eagles the week after ice broke up on the Crooked River during both years of the study (23 before ice break-up to 43 after in 1986, 13 before to 50 after in 1987). W. Elmore (Bur. Land Manage., pers. comm.) also noted increased numbers during the spring thaw. The spring thaw was probably related to the number of eagles observed along the Crooked River because it coincided with a local increase in food (afterbirth from calving, cows and calves that died during calving, ground squirrels, waterfowl, fish) and to the timing of spring bald eagle migration. We also observed that peak bald eagle counts occurred the third week after ground squirrels emerged in both years and that peak counts for the Crooked River occurred the same week as those in the Harney Basin during both years (Oreg. Depart. Fish and Wildl., unpubl. data). Peak bald eagle counts in the Harney Basin have consistently coincided with the northward movement of migrant waterfowl (Isaacs and Anthony 1987) and the departure of eagles from the Klamath Basin (Keister *et al.* 1987) where waterfowl and bald eagles overwinter. Young (1983) documented movement of a marked bald eagle from the Klamath Basin, where it wintered, northward in March, through central and northeastern Oregon. That bird spent a brief period feeding on ground squirrels in northeastern Oregon. All of these observations provide evidence of a relationship between peak counts on the Crooked River and northward migrating bald eagles.

Our weekly population estimate (Figure 2) was based on driving counts and double-survey esti-

mates, because they were made during a single day. The double-survey estimate was probably the most accurate population estimate, because there were always eagles seen from the air that were not observed from the ground and vice versa. The maximum estimate from the double-survey method was 117 eagles on 12 March 1986 (Figure 2). Subadults and eagles in flight or perched at locations other than on the ground or on fenceposts (in junipers, on rimrock, etc.) were often missed during aerial surveys. The ability of eagles to change locations or move onto or off of the study area during the time between air and ground surveys (as much as 1 h) may have affected the estimate of population size by the double-survey technique. The best and most economical method of censusing the population on the Crooked River was the driving count; it could be conducted during a single day, and fewer eagles were missed than by aerial counts.

Peak eagle abundance observed by driving counts during this study (mean = 86, $N = 2$, $SD = 0.7$) was nearly twice that reported for 1979-84 (U.S. Bur. Land Manage., unpubl. data; mean = 44, $N = 6$, $SD = 8.1$). Most of the increase was probably due to increased survey effort as a result of our study. The number of individual bald eagles that used the Crooked River during the winter was probably higher than our maximum counts. Young (1983) observed movements of radio-equipped bald eagles at American Falls Reservoir, Idaho, and speculated that as many as five times the maximum daily count of bald eagles may have used that area for periods ranging from one day to all winter. If this pattern of use exists along the Crooked River, as many as 500 individual bald eagles may pass through and use the area annually.

Prior to this study, we suspected that bald eagles in the Crooked River drainage were birds that had moved north from the Harney Basin. However, simultaneous counts in the two areas (Oreg. Depart. Fish and Wildl., unpubl. data, This study) indicate that bald eagles on the Crooked River were different than those in the Harney Basin. Thus, the 100+ bald eagles observed along the Crooked River substantially increased the number of bald eagles known to utilize eastern Oregon in winter.

Food Habits

Large mammal carrion was the most common food item we observed bald eagles eating. During 1986,

90% of feeding observations ($n = 73$) were at deer (30%), cow (45%), or calf (15%) carcasses; 10% were of eagles feeding on small animals, most of which (5 of 7) were identified as ground squirrels. In 1987, feeding observations were equally divided between large mammal carcasses and small animals (14 each). Two factors contributed to this difference. There were fewer large mammal carcasses available during 1987 (40 in 1987 vs. 130 in 1986) and ground squirrels emerged earlier in 1987 (11 February 1987 vs. 20 February 1986).

The extensive use of mammals for food was substantiated by the composition of intact castings ($n = 251$) found in communal roosts; 89% were composed primarily of fur. In the Harney Basin, waterfowl were the primary food, and 86% of 1,940 castings were composed primarily of feathers (Isaacs and Anthony 1987).

Most carcasses observed ($n = 133$) were deer (49%). Deer carcasses were located nearer public roads than cattle carcasses (mean distance for deer = 51 m, $n = 65$, $SD = 61$; for calves mean = 134 m, $n = 21$, $SD = 128$; for cows mean = 277 m, $n = 47$, $SD = 275$), because most deer died due to collisions with motor vehicles. In contrast, cattle died of natural causes where they were pastured.

Use of carcasses by bald eagles was affected by distance to human activity and carcass condition. Use of carcasses increased with distance from roads (Figure 3a) and was significantly less ($P < 0.05$) than expected for carcasses 0-99 m from roads and significantly more ($P < 0.05$) than expected for carcasses > 149 m from roads. Della Sala *et al.* (1989) found that most bald eagles (73%, $n = 63$) foraged > 50 m from roads in the Willamette Valley where domestic sheep carrion was the primary food. Flushing responses caused by human activity along roads decreased with distance (Figure 3b) and were significantly more ($P < 0.05$) than expected < 50 m from roads and significantly fewer ($P < 0.05$) than expected > 249 m from roads. Stalmaster (1980) and Skaugen (1980) reported similar responses by wintering bald eagles to boating activities along rivers in northwest Washington where salmon carcasses were the primary food. Bald eagles used carcasses that had flesh and viscera exposed more than expected (Figure 3c); carcass use was significantly less ($P < 0.05$) than expected for apparently intact and stripped (appeared to have little or no meat remaining) carcasses.

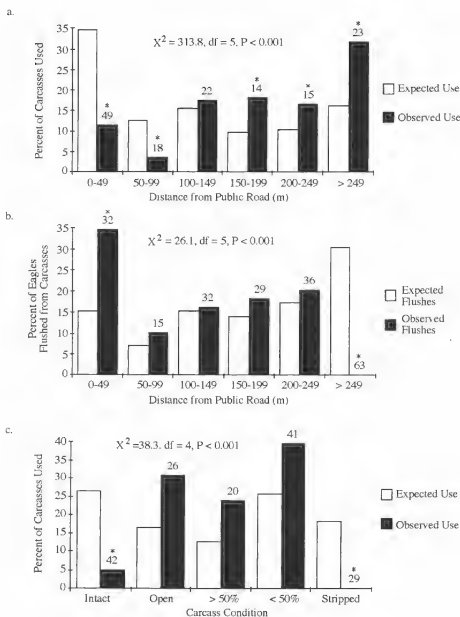


Figure 3. Bald eagle use of large mammal carcasses by distance from public roads and carcass condition along the Crooked River, Oregon, 1986-1987. *Indicates a difference between expected results and observed results ($P < 0.05$) using Chi-square goodness-of-fit tests and Bonferroni confidence intervals (Byers *et al.* 1984). Numbers on top of the black columns are sample sizes.

There was a shift from use of large mammal carrion to small food items in late-February. Only 17 (21%) observations of bald eagles using large mammal carcasses occurred in March and April, even though carcasses were still abundant and the eagle population peaked during that time (Figure 2). Most bald eagle sightings in March and April were near fields with large populations of ground squirrels and near calving areas where stillborn calves and afterbirth were available. Several ranchers allowed the shooting of ground squirrels for target practice, which resulted in high availability of carcasses to scavengers. We saw no evidence that eagles ingested lead when feeding on ground squirrels that had been shot, but believe the potential for lead poisoning exists.

Use of large mammal carcasses by bald eagles could be increased by placing carcasses at least 250 m from areas of human activity. Relocating road-killed deer to isolated areas away from roads would not only enhance feeding opportunities but

would prevent vehicle-induced injuries and mortalities of eagles. Ranchers could increase food by leaving or placing dead livestock at least 250 m from human activity and by not placing carcasses in excavated pits where they were not used by eagles.

The increase in eagle numbers after ice break-up on the river suggested that fish may be another important food. Use of fish could have gone undetected during this study, because fish remains generally do not show up in castings (Mersmann *et al.* 1992) and because eagles feeding on fish in the river channel would have been out of view of many of our observation points.

Roosting Habits and Habitat

Twelve communal night roosts were located at 14 suspected roost areas (Figure 1). Most of the roosts were located during the first seven weeks of the

study. After that, total weekly roost counts were nearly equal to weekly driving counts, indicating that the major roosts used during 1986 and 1987 were known. The maximum straight-line distance from feeding ground to roost was 21 km.

Roosts were generally located in the largest trees in the vicinity of feeding areas and were isolated from human activities. Four roosts were in single trees and eight were in forest stands. Ponderosa pine was the dominant tree species in roosts; 121 of 125 trees measured were ponderosa pine, 3 were Douglas-fir, and 1 was a cottonwood. Ninety-three percent ($n = 1043$) of eagles observed roosting used conifers; 7% used the cottonwood.

Roost and stand tree characteristics were compared for five of the main coniferous roosts (Table 1). Roost trees were larger in diameter ($t = 5.24$, $df = 8$, $P \leq 0.0005$), taller ($t = 2.40$, $df = 8$,

TABLE 1. Characteristics of forest stands and roost trees at five communal roosts used by bald eagles along the Crooked River, Oregon. All trees measured were >30.5 cm diameter at breast height (dbh).

Roost Name	dbh (cm) ^a		Height (m) ^a		Structure ^{a,b} Classification		% of Trees Dead and Dead-topped	
	Stand trees	Roost trees	Stand trees	Roost trees	Stand trees	Roost trees	Stand	Roost
MP 22 Pines	26	2	26	2	26	2		
	68.7	87.6	21.9	28.3	1.7	2.0	8	0
	29.1	19.8	6.6	1.7	1.1	0.0		
Horse Heaven	27	2	27	2	27	2		
	64.6	105.4	20.3	34.0	1.5	2.5	4	0
	22.7	16.2	7.7	5.4	0.9	0.7		
Lower North Fork	37	16	37	16	37	16		
	81.8	94.6	28.2	33.2	1.9	2.9	14	31
	25.4	19.4	6.8	5.7	1.3	1.5		
Upper North Fork	6	2	6	2	6	2		
	68.2	100.3	36.2	40.1	1.7	5.0	0	100
	19.5	12.6	8.9	2.8	0.3	0.0		
Sugar Creek	15	2	15	2	15	2		
	53.7	92.2	26.1	41.0	1.3	2.0	0	0
	16.0	16.1	6.6	2.4	0.4	0.0		
Mean	67.4	96.0 ^c	26.5	35.3 ^c	1.6	2.9 ^c	5	26
Standard Deviation	10.1	7.0	6.3	5.3	0.2	1.2		
t-statistic	t = 5.24		t = 2.40		t = 2.23			
	P $\leq$ 0.0005		P $\leq$ 0.025		P $\leq$ 0.05			

^aValues are: Sample Size / Mean / Standard Deviation.

^b1 = live top with no large dead lateral limbs, 2 = mostly live top with few large dead lateral limbs, 3 = mostly dead top with several large dead lateral limbs, 4 = dead top with large dead lateral limbs and some live lower limbs, 5 = completely dead with large dead lateral limbs (Isaacs and Anthony 1987).

^cMean for roost trees was significantly larger than mean for forest stand trees at $P \leq 0.05$.

$0.010 \leq P \leq 0.025$), and had more open structure ($t = 2.23$, $df = 8$, $0.025 \leq P \leq 0.05$) than forest stands. In addition, the percentage of dead and dead-topped trees was higher in the roost tree sample than in the stand sample (Table 1). The dbh of all coniferous roost trees ($n = 33$; range = 63.5-152.4 cm; mean = 100.4 cm; $SD = 22.7$) was greater than minimum old-growth specifications for the ponderosa pine forest type (53.3 cm dbh; U.S.D.A. Forest Service 1981). These results are similar to forest stand and roost tree characteristics described for the Harney Basin (Isaacs and Anthony 1987), Klamath Basin (Keister and Anthony 1983), and those summarized by Anthony *et al.* (1982) for communal roosts in the Pacific Northwest.

Management Recommendations

1. Exempt roost stands and a 400-m buffer area from commercial timber production and place those areas under a special management strategy (i.e., eagle management areas) with the goal of maintaining large trees (100.4 cm dbh) and an uneven-aged stand condition (Anthony *et al.* 1982). Buffer areas (zones) have been suggested for forest management and for reducing impacts of line-of-sight (in direct view of bald eagles with no vegetative or topographic screening) human activities on bald eagles for nest and roost sites. Anthony and Isaacs (1989) suggest that 400-m buffer zones be established around nest sites "to maintain the integrity of older aged forests" and that human activities be restricted within 800 m of nests during the breeding season in Oregon. Stalmaster and Newman (1978) found that a 300-m buffer zone would eliminate direct responses (flushing) by wintering bald eagles to human activities on the Nooksack River, Washington. Knight and Knight (1984) also studied flushing responses and found that "restriction zones 350 m wide would protect 99% of the wintering eagles perched in shoreline trees" on the Skagit and Nooksack rivers, Washington. McGarigal *et al.* (1991) quantified the effects of agitation (pre-flushing behavioral changes resulting from human activities) on foraging eagles at nest sites on the lower Columbia River, Oregon and Washington. They concluded that 400 and 800-m buffer zones were required to protect 50 and 95%, respectively, of perched bald eagles from agitation and flushing responses. We recommend a 400-m buffer zone around roosts on the Crooked River because most

roosts were shielded from human activity by topographic or vegetative screening within that distance and to eliminate much (50% or more?) of the less obvious, but potentially stressful pre-flushing response to human presence when human activities occur within line-of-sight but outside 400 m. Buffer zone boundaries can be modified during site planning if the specific characteristics of the site (landform, flight paths of eagles to and from feeding areas, screening vegetation, etc.) enable modifications that do not compromise the security of the roost area.

2. Restrict human activities within eagle management areas during the season of use (usually October through April).

3. Prepare site-specific management plans for roosts. Effective planning requires familiarity with the physical characteristics of the site, the way bald eagles use the habitat (flight paths, foraging areas, staging areas, hunting perches, roost trees, etc.), and the landowner's needs.

4. Manage potential roosting areas adjacent to currently-used roosts to provide alternative roosting sites and insure against catastrophic loss of roost stands.

5. Monitor roost use annually and continue searching for new roosts. Roosts are usually associated with feeding areas, so different roosts may be used if changes in food distribution or abundance occur.

6. Maintain large trees in the river valley for both day perching and night roosting. Plant fast-growing deciduous trees with horizontal limb structure (e.g., cottonwood) in or near riparian zones and at least 400 m from areas with concentrated human activity to provide future roosting and perching sites. Protect riparian areas from grazing by livestock to protect plantings and to promote natural revegetation.

7. Conduct driving surveys each winter to determine annual timing and magnitude of peak abundance. Coordinate with similar counts in the Harney and Klamath Basins to monitor the regional population.

8. Use non-poisonous ground squirrel control measures to prevent secondary poisoning of bald eagles feeding on carcasses.

9. Investigate the importance of fish in the diet of bald eagles along the Crooked River prior to initiating projects that could affect the fishery in the Crooked River drainage.

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Literature Cited

- Anthony, R. G., R. L. Knight, G. T. Allen, B. R. McClelland, and J. I. Hodges. 1982. Habitat use by nesting and roosting bald eagles in the Pacific Northwest. *Trans. N. Amer. Wildl. Nat. Res. Conf.* 47:332-342.
- Anthony, R. G., and F. B. Isaacs. 1989. Characteristics of bald eagle nest sites in Oregon. *J. Wildl. Manage.* 53:148-159.
- Byers, C. R., R. K. Steinhorn, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48:1050-1053.
- DellaSala, D. A., C. L. Thomas, and R. G. Anthony. 1989. Use of domestic sheep carrion by bald eagles wintering in the Willamette Valley, Oregon. *Northw. Sci.* 63:104-108.
- Franklin, J. R., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S.D.A., Forest Serv., Gen. Tech. Rep. PNW-8. Pac. Northw. For. Range Exp. Sta., Portland, Oregon. 417 pp.
- Isaacs F. B., and R. G. Anthony. 1987. Abundance, foraging, and roosting of bald eagles wintering in the Harney Basin, Oregon. *Northw. Sci.* 61:114-121.
- Keister, G. P., Jr., and R. G. Anthony. 1983. Characteristics of bald eagle communal roosts in the Klamath Basin, Oregon and California. *J. Wildl. Manage.* 47:1072-1079.
- Keister, G. P., Jr., R. G. Anthony, and H. R. Holbo. 1985. A model of energy consumption in bald eagles: An evaluation of night communal roosting. *Wilson Bull.* 97:148-160.
- Keister, G. P., Jr., R. G. Anthony, and E. J. O'Neill. 1987. Use of communal roosts and foraging areas by bald eagles wintering in the Klamath Basin. *J. Wildl. Manage.* 51:415-420.
- Knight, R. L., and S. K. Knight. 1984. Responses of wintering bald eagles to boating activity. *J. Wildl. Manage.* 48:999-1004.
- Magnusson, W. E., G. J. Caughley, and G. C. Grigg. 1978. A double-survey estimate of population size from incomplete counts. *J. Wildl. Manage.* 42:174-176.
- Breese, S. Carter, G. Kessel, M. LeBlanc, L. Lent, D. Lichter, V. Nicks, D. Sciery, C. Steck, B. and D. Thomas, and E. and A. Wiersch. Lenny Young, George Keister, Kenneth Kardong, and two anonymous reviewers provided valuable comments on the manuscript. This study was conducted under the auspices of the Oregon Cooperative Wildlife Research Unit; Oregon State University, Oregon Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the Wildlife Management Institute cooperating. This is Oregon State University Agricultural Experiment Station Technical Paper No. 9028.
- Mersmann, T. J., D. A. Buehler, J. D. Fraser, and J. K. D. Seegar. 1992. Assessing bias in studies of bald eagle food habits. *J. Wildl. Manage.* 56:73-78.
- McClelland, B. R., L. S. Young, D. S. Shea, P. T. McClelland, H. L. Allen, and E. B. Spettigue. 1982. The bald eagle concentration in Glacier National Park, Montana: Origin, growth, and variation in numbers. *Living Bird* 19:133-155.
- McGarigal, K., R. G. Anthony, and F. B. Isaacs. 1991. Interactions of humans and bald eagles on the Columbia River estuary. *Wildl. Monogr.* 115. 47 pp.
- Skagen, S. K. 1980. Behavioral responses of wintering bald eagles to human activity on the Skagit River, Washington. *In* R. L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen, eds. *Proc. Wash. Bald Eagle Symp. The Nature Conservancy, Seattle.* Pp. 231-241.
- Stalmaster, M. V. 1980. Management strategies for wintering bald eagles in the Pacific Northwest. *In* R. L. Knight, G. T. Allen, M. V. Stalmaster, and C. W. Servheen, eds. *Proc. Wash. Bald Eagle Symp. The Nature Conservancy, Seattle.* Pp. 49-67.
- Stalmaster, M. V., and J. R. Newman. 1978. Behavioral responses of wintering bald eagles to human activity. *J. Wildl. Manage.* 42:506-513.
- Stalmaster, M. V., J. R. Newman, and A. J. Hansen. 1979. Population dynamics of wintering bald eagles on the Nooksack River, Washington. *Northw. Sci.* 53:126-131.
- U.S.D.A. Forest Service. 1981. Pacific Northwest Regional Plan Draft. U.S. Dep. Agric., For Serv., Portland, Oregon. 98 pp.
- U.S. Department of Interior. 1978. Determination of certain bald eagle populations as endangered or threatened. *Fed. Register* 43:6230-6233.
- Ward, P., and A. Zahavi. 1973. The importance of certain assemblages of birds as "information centres" for food finding. *Ibis* 115:517-534.
- Young, L. S. 1983. Movements of bald eagles associated with autumn concentrations in Glacier National Park. *Univ. Montana, Missoula. M.S. Thesis.* 102 pp.

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J. Stevenson Macdonald, Department of Fisheries and Oceans, Biological Sciences Branch, West Vancouver Laboratory, West Vancouver, British Columbia, Canada V7V-1N6

and

Blythe D. Chang, Department of Fisheries and Oceans, Biological Station, St. Andrews, New Brunswick, Canada E0G-2X0

Seasonal Use by Fish of Nearshore Areas in an Urbanized Coastal Inlet in Southwestern British Columbia

Abstract

In this study, we examine the seasonal variation in fish assemblages at three nearshore marine sites on the north shore of outer Burrard Inlet, British Columbia. Monthly collections with beach seines were made to document changes in species abundance, fish size, and feeding activities over the period of one year. Collection sites represented the shallow sloping cobble beaches common to the Burrard Inlet area. Such beaches are frequently dyked, filled or dredged for port facilities during urban development. A total of 29 species were caught, including juvenile salmonids (*Oncorhynchus* spp.); chum salmon (*O. keta*) was the most abundant salmonid. Fish were caught throughout the year, but more individuals and species were present in the spring and summer than at other times. A size increase over time was noted for many of the species, and stomach analyses indicated that fish were feeding throughout the period they were present. Prey was planktonic or epibenthic and in general originated from marine sources. Outer Burrard Inlet functions as a temporary early marine residence and/or nursery region for many local fish despite local urbanization pressure from metropolitan Vancouver. The destruction or degradation of such areas can have harmful effects on fisheries resources.

Introduction

For over a century, estuaries and nearshore marine habitats of the northeastern Pacific coast have been subject to numerous environmental impacts due to industrial, commercial, and residential development. These areas are also important for foraging, predator avoidance, and physiological transition by various fish species, including Pacific salmon (*Oncorhynchus* spp.), particularly chum (*O. keta*) and chinook (*O. tshawytscha*) (Simenstad *et al.* 1982a, Levy and Northcote 1982). The Fraser River Estuary and adjacent Burrard Inlet support important fish resources, including Pacific salmon, Pacific herring (*Clupea harengus pallasii*), many groundfish species, shrimp, and crabs (Nelles 1978). Recently however, much of the habitat on which these species depend has been altered or lost to urbanization of greater Vancouver and fish stocks have declined (Harris 1978, Fedorenko and Shepherd 1984). Aquatic environments in the lower Fraser River region will continue to be subjected to development proposals which can affect both the physical habitat and water quality of the nearshore environment and adjacent streams.

Data on the use of these environments by fish is needed in order to assess and predict the effects of development on fisheries resources. A number of recent studies have examined fish assemblages and habitat use of the Fraser River estuary (North-

cote *et al.* 1979, Greer *et al.* 1980, Gordon and Levings 1984), but only limited, and frequently unpublished information, is available regarding fish use of Burrard Inlet (Waters 1986).

In this study we examine the seasonal variation in fish assemblages at three nearshore sites on the north shore of the outer basin of Burrard Inlet. Sample sites chosen typify the shallow sloping beach habitat that composes most of the unaltered portion of the basin's shoreline. Our objective was to compose a resource inventory, including information on the numbers, species and sizes of fish, and to gather information on the source of food and degree of feeding activity of fish present in this habitat. Ultimately, we wish to describe the value of this habitat to our local fish stocks and identify the periods of highest sensitivity when fish migration rate and/or juvenile fish abundance is high (nursery periods). This information is required to establish guidelines for nearshore development.

Study Area

Burrard Inlet (49°18'N, 123°15'W) extends for about 31 km from its mouth at the Strait of Georgia to its head at Port Moody (Figure 1A). The following description is adapted from Thomson (1981). The inlet is divisible into inner and outer basins by a narrow body of water (First Narrows, Figure 1A). The outer basin, at its maximum, has

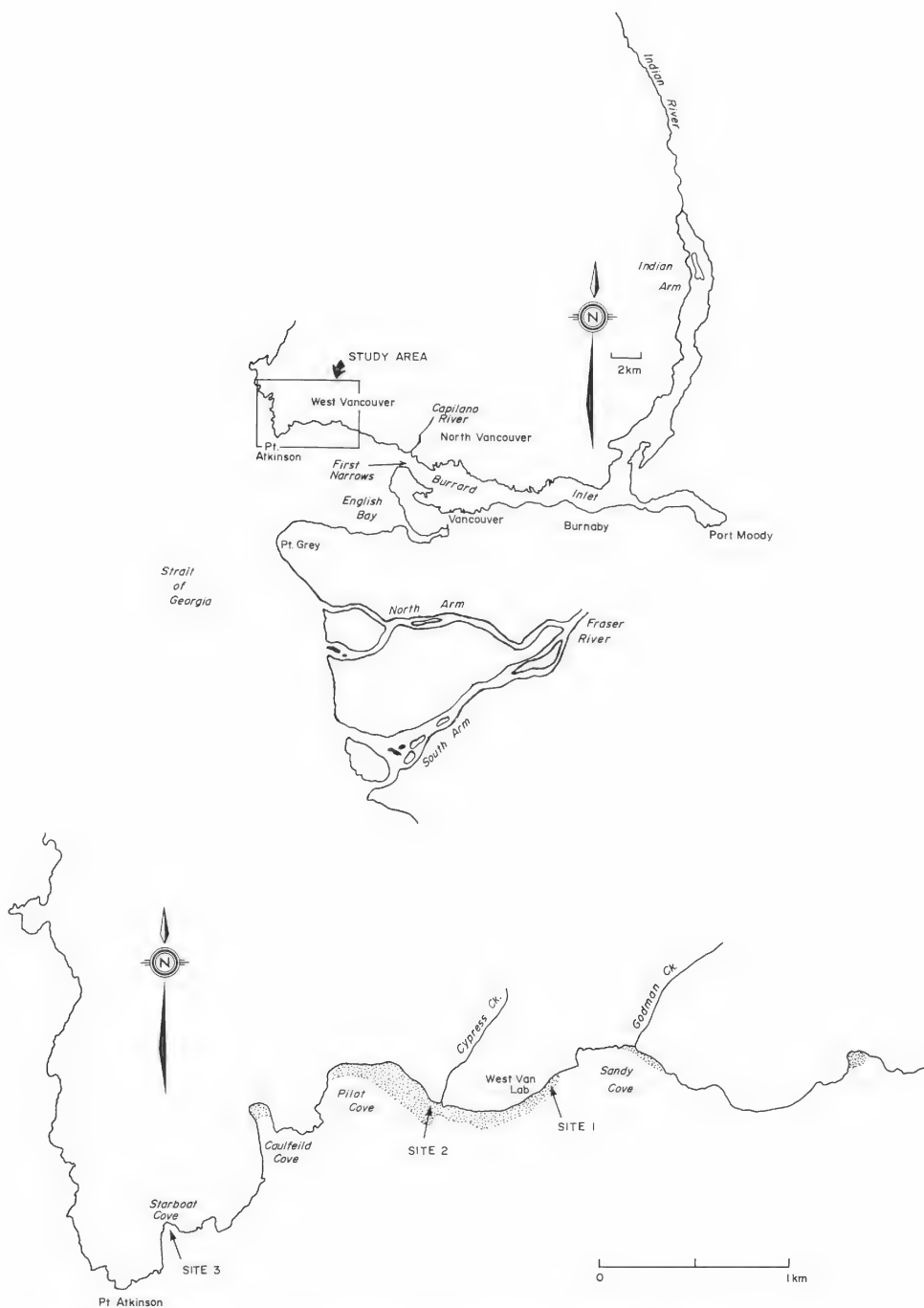


Figure 1. Map of Burrard Inlet and Indian Arm (1A), with sample site locations indicated (1B).

a width of 7 km and extends for about 9 km from Point Atkinson east to the First Narrows. It is bordered by residential areas of Vancouver on the south and West Vancouver on the north. The inner basin is up to 3.5 km wide and extends east from the First Narrows through the highly industrialized and commercialized areas of Vancouver Harbour. Indian Arm extends north for 22 km from near the head of Burrard Inlet in a largely undeveloped area.

The outer basin of Burrard Inlet receives most of its fresh water from the North Arm of the Fraser River, which discharges into the Strait of Georgia 7 km to the south. The peak runoff period for the Fraser River is from May to July. The main direct freshwater input to the outer basin of Burrard Inlet is the Capilano River, which discharges to the north shore of the outer basin about 6 km east of the study area.

The three sites sampled in this study were located on the north shore of the outer basin between Point Atkinson and Sandy Cove (Figure 1B). The adjacent land use is predominantly residential.

Fish Resources of Burrard Inlet

Salmon spawning has been observed in 16 streams flowing into Burrard Inlet (Farwell *et al.* 1987). Between 1981 and 1985, the number of adult salmon returning to these streams (including hatchery returns) averaged 1,200 chinook, 26,000 chum, 32,000 coho (*O. kisutch*), 25,600 pink (*O. gorbuscha*), and 13 sockeye salmon (*O. nerka*). The majority of the chinook (74%) and coho (65%) were hatchery salmon returning to the Capilano River, while most of the chum (97%) and pink (96%) salmon were naturally spawned fish returning to the Indian River. Pink salmon do not return to these streams in even numbered years. Annual steelhead (*O. mykiss*) returns to Burrard Inlet streams averaged 840 during 1981-1983, including some hatchery production (Department of Fisheries and Oceans, unpublished data).

In 1983 the Capilano River Hatchery released 522,000 yearling coho (average weight 15.2 g), and 798,000 underyearling chinook salmon (average weight 8.2 g). Thirty-two percent of both species of fish were marked with a coded wire nose tag and an adipose fin clip. The juvenile coho salmon were released on June 1. The juvenile chinook salmon were released on June 8 to 10 (Capilano hatchery staff, personal communication).

Additional juvenile salmonids immigrate into Burrard Inlet and Vancouver Harbour in the spring, from the Fraser River system and possibly from Puget Sound and Vancouver Island streams (Nelles 1978; Conlin, unpublished report).

Few fish surveys have been done in Burrard Inlet, and those that have provide limited interpretation and are restricted to the summer months. They describe the Inlet as having a diverse and abundant assemblage of fish species. Purse and beach seines, and hydroacoustic surveys by Nelles (1978) estimated 1000-2000 tons of Pacific herring (0+) in Vancouver Harbour in late August 1973. Subtidal bottom trawl surveys commonly catch English sole (*Pleuronectes vetulus*), rex sole (*Ernex zachirus*), flathead sole (*Hippoglossoides el-lasodon*) and hybrid sole (*Inopsetta ischra*) (Thomas and Goyette 1987). Levings (1973) identified 37 fish species, most of which were juvenile flatfish, suggesting that shallow areas in Burrard Inlet may act as nursery grounds.

Methods

Sampling Sites Characteristics

Three sites along the north shore of Burrard Inlet were sampled (Figure 1B). Site one was an exposed gravel beach located adjacent to the pilings, docks and rip-rap associated with the West Vancouver Federal Laboratory of the Canadian Department of Fisheries and Oceans. Site two was near the midpoint of a two km gravel beach that was exposed to S.E. swells. Cypress Creek, a small stream that supports a small run of coho salmon (average annual return of seven from 1981-1985; Farwell *et al.* 1987), enters the Inlet immediately to the east of this sampling site. Site three was a sheltered gravel beach located at the head of a small cove near Point Atkinson within a region of rocky headlands at the mouth of Burrard Inlet. It was the only site that could be seined efficiently within these headlands.

Surface water temperatures during sampling ranged from 8-9°C in winter (February, March, November) to about 16-17°C in summer & June-September, Figure 2). Salinity was not measured in this study. Despite the proximity of site two to a small creek, none of the sampling sites received large freshwater runoff from the adjacent land. Surface salinities in the vicinity of our study area range from approximately 20‰ in summer to approximately 25‰ in winter (Thomson 1981).

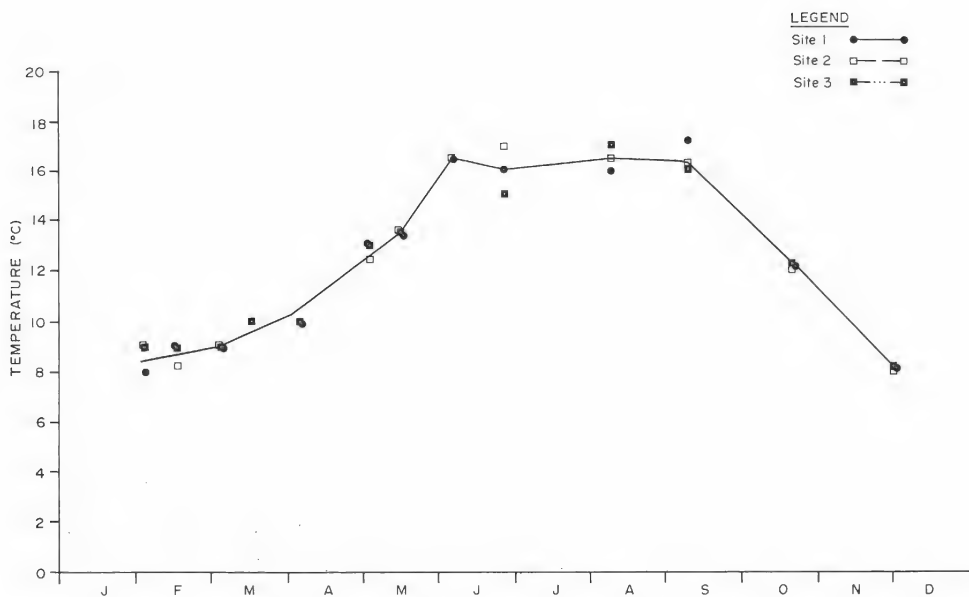


Figure 2. Surface water temperatures at sample sites during sampling times in 1983. Line is fit through all points by eye.

Sampling Methods

Fish were sampled using a 13.8 m beach seine with 4.6 m wings (10 mm stretched mesh), a 4.6 m bunt (5 mm stretched mesh), and a 3.0 m depth. The net was fitted with a 15 m towing line attached to each wing, with which it was pulled off the beach using an outboard powered 5 m inflatable boat. Once the net was approximately 10 m offshore and parallel to the beach it was immediately hauled in. With this method we were able to consistently sample an area of approximately 100 m². Sampling was done at intermediate tide levels (2.0-3.5 m), and usually in the early afternoon.

Thirteen sampling trips were undertaken between 4 February and 30 November 1983. Two replicate beach seine sets were made adjacent to each other at each site. A total of 76 sets were made during the study. Due to adverse weather conditions, Site three was not sampled during the 7 June trip.

At each site, fish were removed from the net and counted into buckets filled with seawater. Lengths of all species of fish were recorded. Subsamples ($n = 20-30$) were used to estimate lengths when catch size of a species exceeded 50 individuals. Fork lengths were used if species had

indented caudal fins. Otherwise, maximum total lengths were used. Subsamples, to a maximum of 10 individuals of each species caught, were preserved immediately in 10% formalin. Stomachs of the larger fish were injected with formalin using a needle and syringe.

Catch per unit effort (CPUE) was estimated as the average catch per seine haul at each site, during each sampling time. The nine of the most common species of fish were selected for length-frequency distribution and stomach content analyses (species chosen are listed in Table 1). Comparisons of lengths among sites were made for each of the nine species of fish using analysis of covariance (ANCOVA, SAS Proc GLM 1985), which also tested and corrected for the temporal variation in fish length (covariate). Tests for homogeneity of variance and linearity between the dependent and independent variables were made before each statistical test and the data were transformed, if necessary.

Stomach contents were removed in the laboratory, rinsed to remove formalin and preserved in 70% ethanol. Contents of the nine common predator species were identified to family or order, counted and the entire contents of the stomach

TABLE 1. Species list, in order of total abundance, indicating presence (+) or absence (-) at each sampling time with data from all sites combined. Sites at which each species was captured (a = all 3 sites) and the total number caught during the whole study are listed. Nine species were selected for length-frequency and stomach content analyses*, two were selected for stomach content weight comparisons†.

Month: Day:	Sample Date													Site	Total Catch (n)
	02 04	02 17	03 04	03 17	04 05	05 03	05 16	06 07	06 27	08 09	09 09	10 20	11 30		
Pacific sand lance* †	-	-	+	-	-	+	+	+	+	-	-	-	-	a	1952
Chum salmon* †	-	-	+	+	-	+	+	+	+	+	-	-	-	a	1185
Threespine stickle-back*	+	+	-	+	-	+	+	+	+	+	+	+	-	a	587
Chinook salmon*	-	-	-	-	-	+	+	+	+	+	+	-	-	a	58
English sole*	-	-	+	+	+	+	+	-	-	+	-	+	+	a	49
Speckled sanddab*	-	-	+	+	+	+	+	+	+	+	+	+	+	a	36
Bay pipefish	-	-	-	-	-	+	+	-	+	+	+	-	-	a	35
Starry flounder*	+	-	+	+	+	+	+	+	+	+	+	+	+	a	33
Tidepool sculpin*	+	-	+	-	-	+	+	-	+	+	+	-	-	a	28
Pacific staghorn sculpin	-	-	-	+	+	+	+	+	+	+	+	+	-	a	24
Kelp greenling	-	-	-	-	-	+	+	+	+	+	+	-	-	a	15
Coho salmon*	-	-	-	-	-	-	+	+	-	-	-	-	-	1,2	15
Tube-snout	-	-	+	-	-	-	-	-	+	+	-	-	-	2,3	15
Surf smelt	-	-	+	-	-	-	+	-	-	-	+	+	-	1,2	10
Buffalo sculpin	-	-	-	+	+	+	+	+	-	-	-	-	-	1,2	8
Pile perch	-	-	-	-	-	-	-	+	-	+	-	-	-	2,3	6
Steelhead	-	-	-	-	-	-	+	+	-	-	-	-	-	2	5
Sharpnose sculpin	+	+	-	-	-	-	-	-	-	-	-	-	+	1,2	5
Pacific tomcod	-	-	-	-	-	+	+	-	-	-	-	-	-	3	5
Shiner perch	-	-	-	-	+	-	-	+	-	-	+	-	-	1,2	4
Penpoint gunnel	-	-	-	-	-	-	+	-	-	+	+	-	-	3	3
Crescent gunnel	-	-	-	-	+	+	-	-	-	+	-	-	-	2,3	3
Sockeye salmon	-	-	-	-	-	-	+	-	-	-	-	-	-	1	2
Pacific herring	-	-	-	-	-	-	-	+	+	-	-	-	-	1	2
Rock sole	-	-	+	-	-	+	-	-	-	-	-	-	-	1	2
Dover sole	-	-	-	-	-	-	-	-	+	-	-	-	-	2	1
Butter sole	-	-	-	-	-	+	-	-	-	-	-	-	-	3	1
Eulachon	-	-	+	-	-	-	-	-	-	-	-	-	-	1	1
Northern anchovy	-	-	-	-	-	+	-	-	-	-	-	-	-	3	1

weighed on a top-loading, 2-decimal-place balance. Principal Components Analysis (PCA, SAS Proc Factor 1985) was used to identify the prey categories that occurred in large numbers and to identify those categories that differed in abundance among collection dates and predator species.

The stomach content weights of chum salmon and Pacific sand lance (*Ammodytes hexapterus*) were used to estimate the level of feeding activity by these species, during each collection date at

each site. Other species were not collected in sufficient numbers to allow comparisons (Table 1). Content weights were compared using an ANCOVA which also tested and corrected for the effect that growth-induced increase in fish weight (covariate) had on stomach content weight. Data transformation was not necessary. Beach seine collection times each day were kept consistent to minimize the potential confounding effects caused by diel variation in stomach content composition and weight.

Results

Species Presence

A total of 29 fish species were caught during this study (Table 1). Pacific sand lance, chum salmon, and threespine stickleback were by far the most abundant species, composing 91% of the total catch. The ten most abundant species were caught at all three sites. The difference in species composition among sites were mainly due to the presence or absence of the least abundant species. The numbers of individuals (particularly the rarer species) were insufficient to determine if there were significant differences in species composition among sites. Unless otherwise stated, in all further analyses the data from all three sites were combined.

Five species of juvenile salmon and trout were caught. Chum salmon were by far the most abundant, followed by chinook salmon. One of the 15 coho salmon caught had been tagged, indicating hatchery origin (note that most hatchery-reared coho and chinook salmon juveniles do not receive tags). This fish was caught on 16 May. The coded-wire nose tag indicated it was one of 20,000 coho

that had been released inadvertently from the Capilano hatchery during a flood on 9 March 1983. Two sockeye salmon and five steelhead were also caught.

Seasonal Abundance Changes

Only a few species, such as threespine stickleback (*Gasterosteus aculeatus*), English sole, speckled sanddab (*Citharichthys stigmaeus*), starry flounder (*Platichthys stellatus*), tidepool sculpin (*Oligocottus maculosus*) and Pacific staghorn sculpin (*Leptocottus armatus*), were present throughout most of the year (Table 1). Species richness showed a seasonal trend at all sites, with more species being caught during spring (particularly at sites 2 and 3) and early summer (site 1) (Figure 3). Site 1 had greater species abundance than the other sites during most of the late fall and winter collections. Total fish abundance also showed a seasonal trend, with more individuals being present in spring and summer (Figure 4).

Chum salmon were caught in March and from May to August, with greatest abundance in May-June at a density of approximately 1.5 individuals/m² (Figure 4). Chinook salmon were

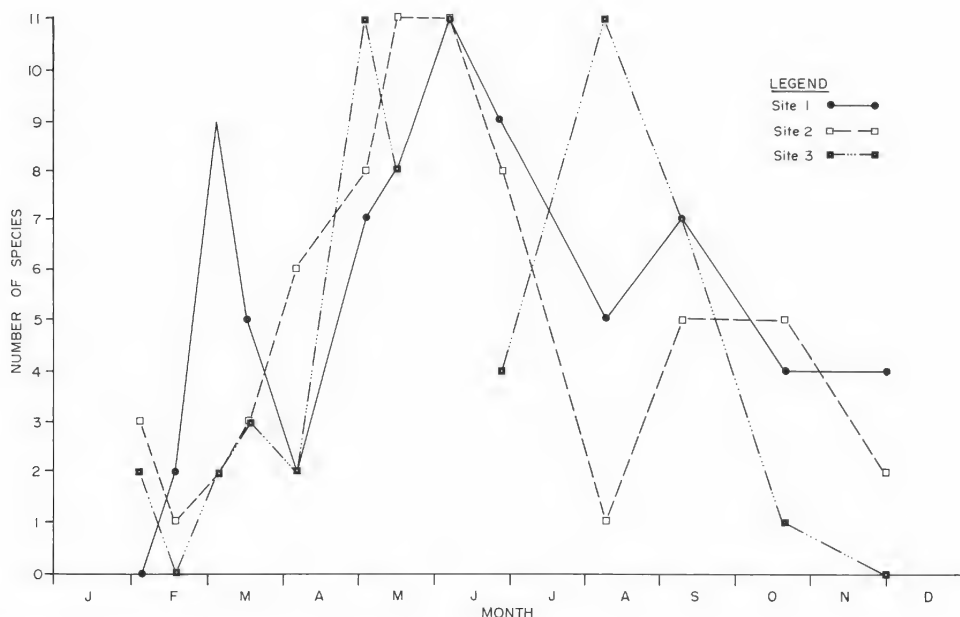


Figure 3. Number of species caught at each sample site in 1983.

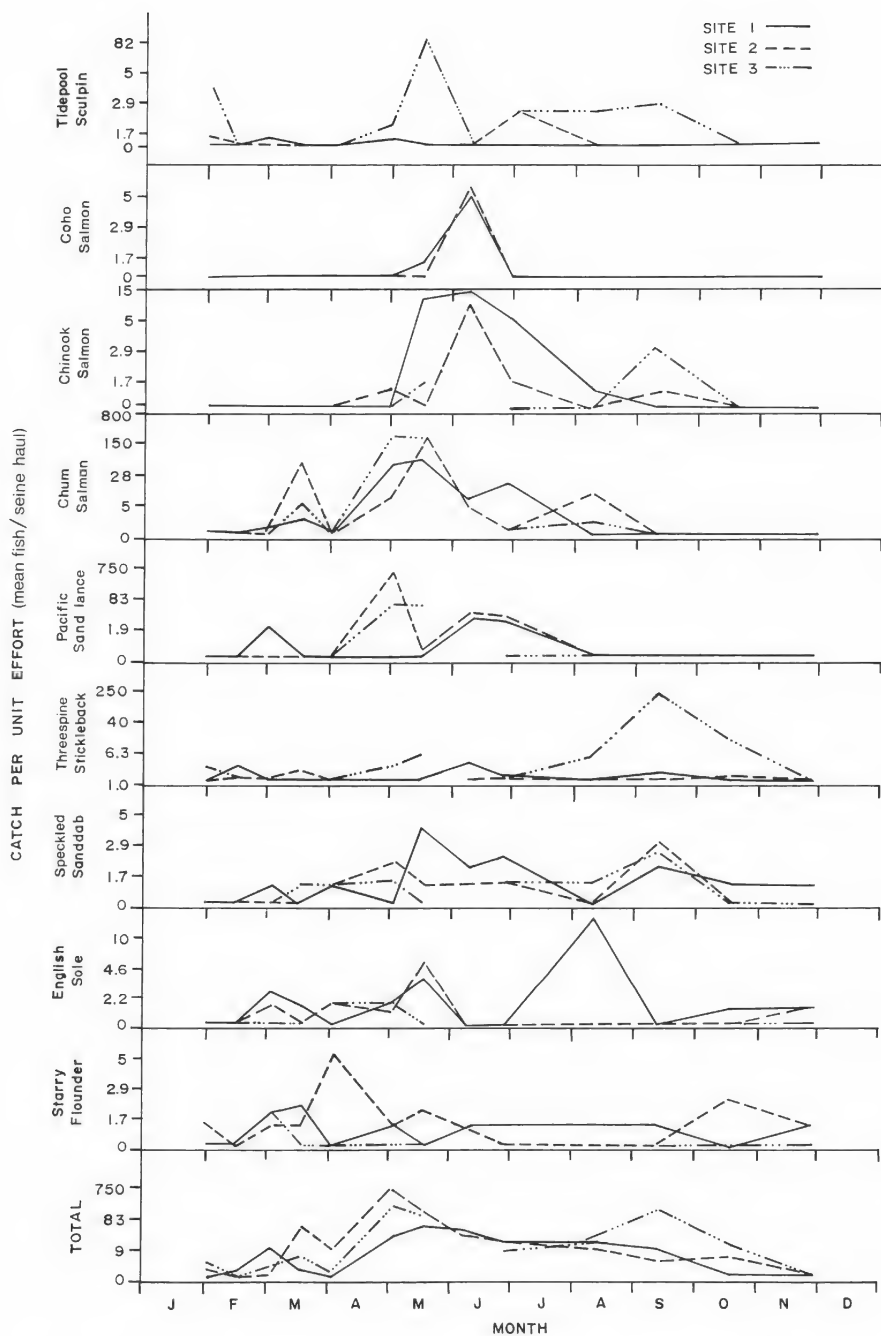


Figure 4. Abundance (catch per unit effort) over time for selected fish species. Each set sampled approximately 100 m² area. Vertical axis is on a logarithmic scale. Site 3 was not sampled on 7 June due to inclement weather.

caught from May to September with a peak density of approximately 0.1 individuals/m² in May and June. Numbers were relatively low in August and September. Coho salmon were caught only on 16 May and 7 June. Sockeye salmon were caught only on 16 May and steelhead were caught in May and June (data not shown).

Pacific sand lance were caught from March to the end of June only, with the highest abundance in early May at a density of approximately 7.5 individuals/m² (Figure 4). This may be an underestimate as sand lance are able to burrow in the sand and potentially avoid capture. Threespine stickleback were caught in relatively low numbers throughout most of the year, with one very large sample in September at Site 3. Seasonal abundance trends for other common species are also shown in Figure 4.

Length-Frequency Distributions

For each of the nine common species, the size of fish captured did not differ among sites during each collection trip ($P > 0.05$). However, meaningful spatial or temporal comparisons of lengths of some fish species are limited by small catch sizes at some sites and times. After combining catches from all sites, and limiting further analysis to the four most common species, variation in length-frequency distributions were detectable ($P < 0.05$), and three of the four species showed temporal trends (chum, sand lance, stickleback; Figure 5). The beach seine may not have been effective at catching small fish, particularly post-larval stages.

The first chum salmon appeared in our samples in March at a length of 31-37 mm (Figure 5). Size increased over time until June, reaching a mean size of 52-55 mm. During this period, the mean length increased at a rate of 0.20 mm•d⁻¹. Chinook salmon first appeared in May as smolts (70-120 mm), but measurements of those caught each month into the fall showed no increase in mean size. Pacific sand lance ranged in size from 25 to 135 mm. The larger sand lance (80-135 mm) were captured from March to May. In May, a second, smaller age class appeared (25-30 mm). Individuals in subsequent collections increased in mean size until June when the fish were nearly the size of those captured in March. The smallest threespine sticklebacks were caught in August (10-25 mm) and mean size increased through the fall. The mean size of the sticklebacks also in-

creased through the spring with the capture of the largest individuals in May.

The other species of salmon captured ranged in size from 60-120 mm for coho, 89-97 mm for sockeye and 134-284 mm for steelhead (data not shown). The tagged coho salmon caught on May 16 was 111 mm in length. Only immature individuals of the four species of sole, tomcod, eulachon, and northern anchovy were caught. Size ranges of other species were: English sole 17-67 mm, speckled sanddab 19-117 mm, Starry flounder 21-430 mm (all but one exceeding 50 mm) and tidepool sculpin 16-94 mm.

Stomach Content Analyses

Thirty-one prey groups were identified in the stomachs of the nine common predator species. Based on the variable loadings on the first three factors of the PCA (describing 94% of the variation in the data matrix), eight prey groups were sufficient to characterize the feeding habits of the predators (Table 2). Food eaten by the fish was either planktonic (e.g., crustacean larvae, calanoid copepods, and *Oikopleura* sp.) or epibenthic (e.g., harpacticoid copepods, amphipods, and cumaceans). Most of the food items resided naturally in marine or estuarine habitats. However, some food items did originate from freshwater sources (e.g., some species of cladocerans). We do not know whether the cladocerans in the diets were consumed during the salmonids' migration from freshwater habitats or were flushed to marine regions before being consumed.

Copepods consumed by chum salmon, tidepool sculpin, and the three species of flatfish were almost exclusively harpacticoids, whereas sand lance and threespine stickleback consumed both calanoid and harpacticoid copepods. Amphipods were consumed by most species during most sampling times (Table 2). Other prey species (e.g., crustacean and decapod larvae, and cumaceans) varied in importance depending on the predator species. Further prey composition comparisons among species were hampered by the small numbers of stomachs examined. The eight coho salmon examined had empty stomachs and very few food items were found in larval fishes' stomachs (e.g., sand lance captured in May).

We were unable to find significant spatial or temporal variation in the amount of food consumed by chum salmon or sand lance ($p > 0.05$).

TABLE 2. Counts per fish of major prey groups of the nine most common predators in the littoral zone of outer Burrard Inlet. Prey groups determined by Principal Components Analysis.

Predator	Chum salmon				Chinook salmon			Coho salmon	Pacific sand lance			Threespine stickle-back	
	Mar.	May	June	Aug	May	June	Aug-Sep	June	Mar	May	June	Feb	May
Copepods	10.4	136.8	0	2.2	0	0.3	0	0	199.0	0	6.7	35.0	8.4
Cladocerans	0	1.9	152.2	0.4	0	0	0	0	0	0	48.3	0	7.1
Other crustacean larvae	0	1.7	0	0	0	0	0	0	0.2	0	0.4	0	114.4
Amphipods	1.0	7.5	1.5	13.5	0	1.1	2.0	0	0.7	0	1.0	0.8	9.1
Decapod larvae	0.6	0	0.5	0	0	4.3	1.0	0	85.2	0	0.3	0	0
Cumaceans	4.0	0.2	18.3	14.9	0	27.1	0	0	0.5	0	0.1	0	0
Cirripedia larvae	0	3.4	0	0	0	0	0	0	0	0	0	0.8	6.3
Oikopleura sp.	0	6.3	0	0	0	0	0	0	2.2	0	0.1	2.3	13.9
Sample size	5	43	4	8	1	7	2	8	4	14	16	4	7

TABLE 2. (cont'd)

Predator	Tidepool sculpin					Starry flounder			English sole			Speckled sanddab			
	Feb	Mar	May	June	Sep	Feb	Apr	May	Apr	May	Nov	Apr	May	June	Sep
Copepods	0.2	16.0	0	0.5	0	0	0.6	0	400.0	101.6	2.0	0	0	0	2.0
Cladocerans	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0
Other crustacean larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipods	2.6	2.0	61.0	1.5	1.0	1.0	10.2	7.0	0	3.4	1.0	13.0	7.8	0	28.2
Decapod larvae	0	0	0.3	0	0	0	0	0	0	0	0	0	0	0	0
Cumacean	0	0	0	0	0	0	0.8	0	5.0	2.6	1.0	0	0.6	0	0.2
Cirripedia larvae	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oikopleura sp.	2.3	0	0	0	0	0	0	0	0	0	0	0	1.6	4.0	0
Sample size	5	1	4	2	1	1	5	2	1	10	1	1	5	3	5

However, larger fish did consume larger meals (as expressed by the covariate stomach content weight; $p < 0.05$) and, for chum in particular, as size increased with time (Figure 5), larger food items became more common in their diet. For example, copepod consumption was greatest early in the year (March-May) and declined with increased consumption of larger prey species such as amphipods and cumaceans (Table 2). However, seasonal variation in the type of food available may also have had an effect on diet.

Discussion

Our study clearly shows use of nearshore marine habitat by fish in outer Burrard Inlet. These sites were used by salmon and other fish species, particularly during the spring and summer when both species abundance and total fish abundance were greatest. Similar trends found by Gordon and Levings (1984) in the Fraser River estuary were correlated to the increased temperatures at this time of year. The 29 species of fish identified in Burrard

Inlet in this study were among the 37 species identified by Greer *et al.* (1980) and the 57 identified by Gordon and Levings (1984), at the mouth of the Fraser River estuary. Inshore fish populations in estuaries around the world typically have modest species diversity with a dominance of the total number of individuals by a few species (Haedrich 1983). Most of the non-salmonid species are of no commercial importance, except for Pacific herring and eulachon (which were rare in our samples) and English sole. However, many of these species, such as Pacific sand lance, starry flounder, kelp greenling (*Hexagrammos decagrammus*), and surf smelt (*Hypomesus pretiosus pretiosus*) are important in the diets of juvenile salmon (Hart 1973) and sea birds (Hay *et al.* 1989).

For the juvenile stages of salmon, sand lance, pile perch and many species of flatfish, the study sites served as a transit area, where temporarily, feeding and other activities associated with rearing (e.g., predator avoidance) likely occur. Juvenile wild and hatchery coho and chinook salmon and steelhead produced in Burrard Inlet streams must pass through Burrard Inlet during their seaward migrations. Juvenile salmon produced in the Fraser River are also known to enter outer Burrard Inlet (K. Conlin unpublished data). Subsequently, the salmon will move offshore (Healey 1980, 1982) and many of the flatfish species will move to deeper water (Ketchen 1956; Hart 1973).

Other species are present in shallow nearshore areas for a substantial period of the year. These were frequently small species such as speckled sanddab, threespine stickleback, sculpins, gunnels and pipefish. Further study of the residence times of individuals of each species is required in order to determine which species remain nearshore for their entire lives. Threespine sticklebacks and Pacific staghorn sculpin are found throughout the year on tidal banks at the mouth of the Fraser River (Gordon and Levings 1984). Presumably, nearshore habitats provide feeding opportunities and protection from predation. However, nearshore populations of prey fishes in midwinter, albeit in lower numbers than in warmer months, may provide an essential food source for birds overwintering in the Strait of Georgia (Vermeer 1983).

Our samples include immature individuals of many species that were also captured as adults. Immature individuals of starry flounder, sand lance, and tidepool sculpins were captured in the spring and early summer, suggesting that the adults

of these species, that were captured in the winter or early spring, were in nearshore waters to spawn (Hay *et al.* 1989). These patterns are consistent with observations of starry flounder on Roberts Bank (Gordon and Levings 1984) and the spawning times reported by Hart (1973). A species closely related to the tidepool sculpin (sharpnose sculpin, *Clinocottus acuticeps*) has been observed spawning in Vancouver Harbour from January through April (Marliave 1981). The immature stages of threespine sticklebacks and speckled sanddabs in Burrard Inlet and threespine sticklebacks at the mouth of the Fraser River (Gordon and Levings 1984) occur in mid summer, suggesting that they spawn during the spring in the Vancouver area. Threespine sticklebacks are reported to spawn from April to September (Scott and Crossman 1973), and may have two spawning peaks (April-May and late August), in marine water near Vancouver (Dr. D. McPhail, University of British Columbia, personal communication).

Juvenile pink salmon were not caught in our study because spawning runs in southern British Columbia generally occur in odd-numbered years, with the downstream juvenile migrations in the following even-numbered years. We would expect significant numbers of juvenile pink salmon in our study area during the spring of even-numbered years (Heard 1991).

The scarcity of juvenile sockeye salmon in our study was expected because adult sockeye escapees to Burrard Inlet streams are very low. The few that we caught during this study may have come from the Fraser River. Juvenile sockeye do not utilize the nearshore marine environment to a great extent (Healey 1980, 1982). Few are found in the littoral zones at the mouth of the Fraser River despite a large sockeye salmon outmigration each spring (Levy and Northcote 1982, Gordon and Levings 1984). Steelhead were also scarce in our study. There are relatively low escapees of steelhead to Burrard Inlet streams, and they may not use nearshore areas for transit to offshore habitats. Increased sampling in different regions is needed to evaluate the importance of Burrard Inlet to steelhead.

Only a small number of juvenile coho salmon were caught in this study, and only in May and June, despite the large numbers that are produced in Burrard Inlet streams (both from natural spawning and hatcheries). While coho salmon fry have been shown to prolong residence in inner estuarine

regions during spring and summer (Tschaplinski 1988), other studies, such as Healey (1980) in the outer Nanaimo River estuary, McCabe *et al.* (1983) in the Columbia estuary and Levy and Northcote (1982) in the Fraser River estuary, have shown that juvenile coho salmon fry and smolts (1+) do not utilize outer estuaries and nearshore marine areas (such as our study area) to a great extent. Coho tagged and released from the Capilano Hatchery were not recaptured six days later during our first sampling trip. They may have remained in the Capilano estuary, or more likely moved offshore, out of reach of our nets. In 1979, Conlin (P. communication) caught several juvenile coho salmon, with Capilano Hatchery tags, at two sites within our study area. However, he found that captures of tagged coho salmon at sites throughout Burrard Inlet dropped off very quickly two to three days after their release from the hatchery. A more intensive sampling schedule may be required to document habitat used by coho and the timing of their outmigration.

In our study, chinook salmon first appeared as 60+ mm smolts in May and were present until September (110+ mm), although numbers were relatively low in August and September. Peak densities in May and June were lower than those reported in Fraser River tidal channels by Levy and Northcote (1982) (0.10 vs. 0.18 individuals/m², using different sampling methods). Similar size ranges and residency periods were observed in shallow marine locations adjacent to the Campbell River estuary (Levings *et al.* 1986), in the outer estuary of the Nanaimo River (Healey 1982) and in the Columbia River estuary (McCabe *et al.* 1983). Chinook salmon in the outer estuary of the Yaquina River estuary, Oregon, are abundant from June to September, although lower numbers were caught through October and November (Myers and Horton 1982).

On the tidal banks at the mouth of the Fraser River, juvenile chinook salmon were first captured in March or April (Gordon and Levings 1984) with peak abundance in May (Conlin *et al.* 1982). Allowing for estuarine residency times of up to 30 days (Levy and Northcote 1982), these fish, and chinook salmon from other nearby systems, could conceivably begin to appear in the adjacent littoral zones of Burrard Inlet in May. The absence of tagged chinook salmon in our study indicates that few, if any, Capilano Hatchery chinook were present when we sampled. However, in Conlin's un-

published study in 1979, tagged juvenile chinook salmon from the Capilano Hatchery were captured at two sites within our study area. Hatchery releases occurred 17-62 d before we began sampling and thus we may have been too late to sample the peak outmigration of these fish from Burrard Inlet. Alternatively, they may have attained a sufficient size to have moved to deeper water, beyond the reach of our nets. Juvenile chinook salmon captured by purse seine off the mouth of the Fraser River had begun to move to deeper water at a length of 50-55 mm; 10 mm longer than those captured by beach seine in shallower water (Levings 1982).

By far the most abundant of the juvenile salmonid species in our study was the chum salmon, present from March to August. There were two peaks in abundance (March and May) during which the density of chum salmon at our sites exceeded that recorded in tidal channels in the lower Fraser River estuary (0.14 vs. <0.60 individuals/m², Levy and Northcote 1982, using a different sampling method). While the two peaks in abundance may be due to sampling variability, they may also reflect different outmigration strategies. A similar pattern in abundance was found by Healey (1982) in the outer estuary of the Nanaimo River. The initial peak in March in our samples may represent juveniles that dispersed seaward immediately after reaching the river mouths (Mar-Apr. in the Fraser River, Levy and Northcote 1982, Gordon and Levings 1984), while the later, larger peak beginning in May may represent juveniles that have reared in estuaries prior to migrating to marine areas. Levy and Northcote (1982) have recorded chum remaining in an estuarine tidal channel complex for up to 11 days. The main peaks in abundance of chum salmon in the outer Fraser and Nanaimo River estuaries and in shallow marine locations in the Gulf Islands (southern Georgia Strait) were also found to occur in May-June (Healey 1980, 1982, Gordon and Levings 1984).

There was a general increase in mean size of juvenile chum in our samples from March (when they first appeared in samples) until early June. We do not know if this was due entirely to growth, since we have no information on the residence times of individual fish at the study sites, although stomach analyses indicated that chum we captured were feeding during the period they were present. The lack of size increase in later samples is probably due to emigration of larger fish to sublittoral and eventually offshore areas.

Emigration from estuarine and marine nearshore areas by chum and chinook salmon is likely related to size (Levings 1982), and possibly abundance, occurring at approximately 5.0-6.0 cm and 12.0-17.0 cm by chum and chinook salmon respectively (Myers and Horton 1982, McCabe *et al.* 1983). During periods of peak fish abundance in areas, when potential competition for limited food resources is highest, offshore movement may be related to availability of preferred prey organisms. Levings (1982) found juvenile Fraser River chinook salmon to feed selectively on the larger items available in the water column. Simenstad and Salo (1982b) suggested the presence of large pelagic copepods in sublittoral areas may explain offshore movement of chum salmon in the Hood Canal, Washington State. However, studies by Gerath (1963), Stockner and Cliff (1979) and unpublished observations of zooplankton population growth by staff of the West Vancouver Laboratory found that zooplankton abundance in outer Burrard Inlet was highest in spring and summer. As the period of greatest fish abundance occurs when food resources are greatest, competition is unlikely to be the main force driving emigration from nearshore areas.

Stomach content analyses in our study indicated that most fish were feeding throughout the period during which they were caught. Meal weight and size of individual prey items increased as the season progressed and the fish grew. This was also observed by Karpenko (1982). Small sample sizes of most fish species and lack of residency time information prevents us from making firm conclusions regarding interspecific diet overlap or the importance of nearshore zones for feeding and growth. However, based on the species of prey identified, it is apparent that a variety of habitats act as a source of food for fish captured in littoral zones. Epibenthic habitats support harpacticoid copepods, cumaceans, and amphipods that are found in the diets of a number of fish species captured in this study, including chum salmon. Other investigators report similar findings (Healey 1979, 1982, Bailey *et al.* 1975, Simenstad and Salo 1982). Food of planktonic origin, commonly found in the diets of sand lance and other species, may have been produced in Burrard Inlet or drifted with tidal currents from other Strait of Georgia locations. Freshwater habitats are also important, providing cladocera and insects found in the stomachs of fish in nearshore habitats. Insects are more important

in diets of fish captured at the mouth of the Fraser River than those captured in our study (Levings 1982).

The study area is located within the metropolitan Vancouver area. The land adjacent to the study sites is a residential area, which is not subject to the more disruptive effects of industries and port facilities located in the inner basin of Burrard Inlet. Nevertheless, waterfront residential areas are subject to development pressures that could alter the nearshore fisheries habitat. Such alterations, including filling of shallow areas, dredging, building of shoreline protection works and construction of marinas, boat launching ramps, seawalls and foreshore parks, can decrease the ability of these areas to support fish. In addition to the threat of physical habitat alteration, nearshore marine areas and creeks adjacent to urban areas are subject to increased threats from pollution, both from land sources and from ships.

This study has shown that nearshore marine areas, such as our sampling sites, are utilized by salmon and other fish species despite urbanization of the adjacent land. While salmon and most other species occupy these areas most heavily in the spring and summer, other species of fish are present throughout the year. These sites serve as nursery areas for the juvenile stages of many fish species, while some species spend their entire lives in these nearshore zones. Most fish that use this zone as a nursery area are likely produced in Burrard Inlet or nearby streams. However, the outer Burrard Inlet region also has some importance as a rearing area for Fraser River salmon stocks, possibly including some of the sockeye, chinook and coho salmon captured during this study (Conlin, unpublished report). While salmon were the only abundant species that were commercially important, other species present may be important to support the salmon's food web and ecosystem. The destruction or degradation of such areas can therefore have significant harmful effects on fisheries resources.

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Literature Cited

- Bailey, J. E., B. L. Wing, and C. R. Mattson. 1975. Zooplankton abundance and feeding habits of fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. *Fish. Bull.* 73(4):846-861.
- Conlin, K. 1980. Distribution of Capilano hatchery chinook in the Capilano Estuary and Burrard Inlet. Unpublished report. 27 p.
- Conlin, K., B. Lawley, P. Futer, M. Kotyk, L. Jantz, B. Hillaby, R. Elvidge, B. Piercey, D. Gordon, C. L. Levings, K. Hutton, R. MacIndoe. 1982. Fraser estuary comparative habitat study: 1. Beach seine catches, water characteristics, and geomorphology March 1980 to July 1981. *Can. Data Rep. Fish. Aquat. Sci.* 340: 125 p.
- Farwell, M. K., N. D. Schubert, K. H. Wilson, and R. C. Harrison. 1987. Salmon escapements to streams entering statistical areas 28 and 29, 1951 to 1985. *Can. Data Rep. Fish. Aquat. Sci.* 601: 166 p.
- Fedorenko, A. V., and B. G. Shepherd. 1984. Review of salmonid resource studies in Indian River and Indian Arm, and enhancement proposals for the area. *Can. MS. Rep. Fish. and Aquat. Sci.* 1769: 30 p.
- Gerrath, J. F. 1963. The monthly abundance of larvae of bottom invertebrates in Indian Arm, British Columbia. B.Sc. Thesis, U.B.C., Vancouver, B.C. 1963.
- Gordon, D. K., and C. D. Levings. 1984. Seasonal changes of inshore fish populations on Sturgeon and Roberts Bank, Fraser River estuary, British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* 1240: 85 p.
- Greer, G. L., C. D. Levings, R. Harbo, B. Hillaby, T. Brown, and J. Sibert. 1980. Distribution of fish species on Roberts and Sturgeon Bank recorded in seine and trawl survey. *Can. MS. Rep. Fish. Aquat. Sci.* 1596: 51 p.
- Haedrich, R. L. 1983. Estuarine fishes, p. 183-203. *In* B. H. Ketchum (ed.), *Estuaries and Enclosed Seas. Ecosystems of the World*; 26. Elsevier Scientific Publishing Co., New York, NY.
- Harris, G. 1978. The salmon and trout streams of Vancouver waters. *Journal of the Vancouver Aquarium* 3(1):4-32.
- Hart, J. L. 1973. Pacific Fishes of Canada. *Fish. Res. Bd. Canada Bull.* 180: 740 p.
- Hay, D. E., M. C. Healey, L. J. Richards and J. B. Marliave. 1989. Distribution, abundance and habitat of prey fishes in the Strait of Georgia. *In* K. Vermeer and R. W. Butler (eds.), *The ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia. Spec. Publ. Can. Wildl. Serv., Ottawa.* Pp. 37-49.
- Healey, M. C. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary: I. Production and feeding rates of juvenile chum salmon (*Oncorhynchus keta*). *J. Fish. Res. Board Can.* 36:488-496.
- . 1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* W. J. McNeil and D. C. Himsforth (ed.) *Salmonid Ecosystems of the North Pacific*. Oregon State Univ. Press, Corvallis, Oregon. Pp. 203-229.
- . 1982. Juvenile Pacific salmon in estuaries: the life support system. *In* V. S. Kennedy (ed.) *Estuarine Comparisons*. Academic Press, New York. Pp. 315-341.
- Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In* C. Groot and L. Margolis (ed.) *Pacific Salmon Life Histories*. U.B.C. Press, Vancouver. Pp. 119-230.
- Karpenko, V. I. 1982. Diurnal feeding rhythm of young salmon during the initial stage of marine life. *J. Ichthyol.* 22(2):131-134.
- Ketchen, K. S. 1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. *J. Fish. Res. Bd. Canada* 13:647-694.
- Levings, C. D. 1973. Sediment and abundances of *Lycodopsis pacifica* (Pisces, Zoarcidae) near Point Grey, B.C., with catch data for associated demersal fish. *Fish. Res. Bd. Can. Tech. Rep. Ser.* 393: 15 p.
- . 1982. Short term use of a low tide refuge in a sand-flat by juvenile chinook (*Oncorhynchus tshawytscha*), Fraser River estuary. *Can. Tech. Rep. Fish. Aquat. Sci.* 1111: 33 p.
- Levings, C. D., C. D. McAllister, and B. D. Chang. 1986. Differential use of the Campbell River estuary, British Columbia, by wild and hatchery-reared juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 43:1386-1397.
- Levy, D. A., and T. G. Northcote. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. *Can. J. Fish. Aquat. Sci.* 39:270-276.
- Marliave, J. B. 1981. High intertidal spawning under rockweed, *Fucus distichus* by the sharpnose sculpin (*Clinocottus acuticeps*). *Can. J. Zool.* 59(6):1122-1125.
- McCabe, G. T., Jr., W. D. Muir, R. L. Emmett and J. T. Durkin. 1983. Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River estuary. *Fish. Bull.* 81(4):815-826.
- Myers, K. W. and H. F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon. *In* U. S. Kennedy (ed.) *Estuary Comparisons*. Academic Press, London, England. Pp. 377-392.
- Nelles, S. 1978. Comments on juvenile salmonid utilization of Burrard Inlet and Vancouver Harbour. Fisheries and Marine Service Internal Report. Dept. Fisheries and Environment, Vancouver. 20 p.
- Northcote, T. G., N. T. Johnson, and T. Tsumara. 1979. A regional comparison of species distribution, abundance, size and other characteristics of lower Fraser River fishes. Westwater Research Centre, University of British Columbia, Vancouver, B.C. Tech. Rep. 14.
- SAS Institute Inc. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute Inc., Cary, NC. 965 p.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. *Fish. Res. Bd. Canada Bull.* 184: 966 p.
- Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982a. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: An unappreciated function. *In* V. S. Kennedy (ed.) *Estuarine comparisons*. Academic Press, London, England. Pp. 343-364.
- Simenstad, C. A. and E. O. Salo. 1982b. Foraging success as a determinant of estuarine and nearshore carrying capacity of juvenile chum salmon (*Oncorhynchus keta*) in Hood Canal, Washington. *Alaska Sea Grant Rep.* 82-2: 21-37.
- Stockner, J. G., and D. D. Cliff. 1979. Phytoplankton ecology of Vancouver Harbour. *J. Fish. Res. Bd. Canada* 36:1-10.

- Thomas, M. and D. Goyette. 1987. Vancouver Harbour benthic environmental quality studies May 1985 to September 1986. Relative species abundance and distribution—trawl catch. Environment Canada, Conservation and Protection, Environmental Protection, Pacific and Yukon Region, Regional Data Report DR87-03: 63 p.
- Thomson, R. E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56: 291 p.
- Tschaplinski, P. J. 1988. The use of estuaries as rearing habitats by juvenile coho salmon. In T. W. Chamberlin (ed.) Proceedings of the Workshop: Applying 15 years of Carnation Creek results. Pacific Biological Station, Nanaimo, British Columbia. Pp. 123-142.
- Vermeer, K. 1983. Marine bird populations in the Strait of Georgia; comparison with the west coast of Vancouver Island. Can. Tech. Rep. Hydrogr. Ocean Sci. 19. 18 p.
- Waters, R.D. 1986. Initial environmental assessment profile of Vancouver Harbour. Can. Environmental Protection Service. Regional Manuscript Report 85-06: 30 p.

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Maturity of Lake Trout from Eleven Lakes in Alaska

Abstract

This study was undertaken to estimate the length and age at which lake trout *Salvelinus namaycush* become sexually mature in a variety of lakes in Alaska. Probit analysis was used to estimate length and age at first, median, and complete maturity for lake trout from 11 populations. Ages at which lake trout matured among the populations were quite variable. Ages at 50% maturity for females ranged from 4.9 to 14.3 years. Males generally matured at a younger age than did females. The estimates of age at maturity were within the range of estimates reported from other areas. Estimates of length at maturity were less variable among the populations studied. Lengths at 50 percent maturity for females ranged from 348 to 481 mm FL and have a positive correlation to lake surface area. The estimates of length at maturity for lake trout from these Alaskan lakes were generally less than those reported from other areas. The effects of latitude, altitude, lake size and available forage on the sexual maturity of lake trout are examined. Length limit regulations applied to lake trout populations in lakes of greatly different surface area sizes, even within a small geographical area, are unlikely to be effective at providing adequate protection for lake trout from harvest through at least one spawning.

Introduction

The length and age at which lake trout *Salvelinus namaycush* become sexually mature are indicative of growth rates, productivity, and food habits of a population (Martin 1952), which in turn affects the reproductive potential and sustainable yield. In addition, populations composed of small, rapidly maturing lake trout may provide greater yield in numbers than do populations of later maturing larger fish (Martin 1966). Consequently, fishery management regulations designed to protect immature and first spawning fish in a population of lake trout through minimum length limits or the spawning stock with a slot limit must address differences in size at maturity. Information about maturity of lake trout and the criteria for classifying a fish as mature or immature is often not well defined (Healey 1978). Other than those fish which are in spawning condition, designating a fish as mature or immature in the field can be subjective and relies heavily on the experience of the examiner, particularly for younger and smaller fish (Martin and Olver 1980).

The age and length at sexual maturity is variable among populations of lake trout. Slow growing populations may not mature until ages 13-17 (Miller and Kennedy 1948). In most naturally reproducing populations, maturity does not occur until age 5 for males and ages 6-8 for females (Martin and Olver 1980). Females reared in experimental ponds (Surber 1933) or stocked (Hanson and Wickwire 1967, Olver and Lewis 1977) have occasionally been reported to spawn at age 4. Male

lake trout from planktivorous populations were mature at age 4 with females mature at age 5 or older (Martin 1966, Donald and Alger 1986). Reported lengths at maturity vary from 180 mm for males and 200 mm for females in Sassenach Lake (Donald and Alger 1986) to lengths in excess of 600 mm (Seneca Lake, Royce 1943; Lake Superior, Eschmeyer 1955; and Lake Simcoe, MacCrimmon and Skobe 1970).

Little is known about the age and length at which lake trout mature in Alaska, the western extent of the native range of the species. Lake trout in Itkillik, Campsite, and Old John Lakes (68° latitude) mature between 10 and 14 years of age (otoliths) and between 340 and 430 mm FL (McCart *et al.* 1972; Craig and Wells 1975). Farther south (63° latitude), most lake trout in Paxson and Summit Lakes were mature at 7 to 10 years of age (scales), and at lengths of 450 to 490 mm FL (Van Wyhe and Peck 1968).

In 1987, harvest limits for lake trout were reduced in most areas of Alaska and a minimum length limit was adopted for some lake trout fisheries. The goal of the minimum length limit was to permit lake trout to spawn at least once prior to legal harvest. A single size limit (18 inches TL, 420 mm FL) was applied to roadside lakes ranging in size from 150 to more than 1,500 ha. This study was conducted to determine age and length at maturity for lake trout from a variety of lakes in Alaska and to evaluate if the length limit regulation provided adequate protection for lake trout from harvest through at least one spawning.

Methods

Data on length, age, and maturity were collected from lake trout in nine lakes in the Alaska Mountain Range in central Alaska and from two lakes in the Brooks Mountain Range of arctic Alaska (Figure 1). All lakes except Paxson Lake and Walker Lake are above tree line (Table 1). Lake trout were collected with small mesh, sinking, gill nets measuring 60 m X 3 m and with mesh size of 25 mm and 38 mm square measure. Samples were collected during mid June through September, 1987-1990. All fish were measured to the nearest mm fork length (FL) and were dissected to obtain otoliths (sagittae). Sex and state of maturity were determined by field inspection of gonads.

Females containing eggs with diameters greater than 1 mm and ovaries with stretched, fragmented mesovarium were considered mature (Martin and Olver 1980). The presence of retained eggs was used to identify females which had spawned previously. Females with tightly compacted and granular ovaries that contained eggs less than 1 mm in diameter were considered immature. Males with flattened testes with a maximum width of 3 mm or more were considered mature. Males with testes which were cylindrical in cross section and less than 3 mm in diameter were considered immature.

Ages were determined from otoliths. Whole otoliths were cleared in a solution of glycerine, ethyl alcohol, and water and viewed with a dissecting microscope with moderate power (12x-50x) under reflected light (Sharp and Bernard 1988). The hyaline or translucent bands were used as annuli and the annuli were counted from the nucleus outward (Nordeng 1961). When necessary, a portion of the lateral surface was removed by hand grinding on a carborundum stone. Some of the oldest samples (age 15 or greater) required additional preparation. The outer annuli in these samples were very closely spaced and were indistinct when the whole otolith was viewed laterally (sagittal plane). In these cases, the otoliths were sectioned through the nucleus with the aid of a Dremel tool, and the otoliths were viewed in cross section. The nucleus of the otolith was clearly visible and the outer annuli were distinct.

The proportion of mature and immature lake trout of each sex from each population was determined for each age class and for 25 mm length categories. More than one age or length category generally contained mature and immature fish.

Probit analysis was used to estimate the median age (AM_{50}) and length (LM_{50}) at maturity (Finney 1971; Tripple and Harvey 1991). The same samples were used for analysis of maturity at both age and length. The midpoints of the 25 mm fork length intervals were used for computations of maturity at length. Estimates of 5% and 95% maturity from the probit analysis were used for first and complete maturity. The numbers of lake trout of each sex sampled from each population are given in Figure 2.

Comparison of 95% fiducial limits from the probit analysis was used to determine if estimates of maturity were different between sexes and between populations. Estimates were considered different when there was no overlap in the fiducial limits.

Results

Estimates of age at which 50% of female lake trout matured (AM_{50}) in the eleven populations sampled ranged from 4.9 to 14.3 years (Figure 2). Males generally matured at younger ages than did females. However, because of overlap in the fiducial limits around estimates of AM_{50} for males and females, only males and females from Paxson Lake were considered statistically different. The estimated age at first maturity (AM_5) for females varied from 4.9 years in Paxson Lake to 11.0 years in Walker Lake (Figure 2). Estimates of first maturity for males were generally about one year earlier than for females but as with most of the estimates of AM_{50} , were not considered statistically different. Estimates of the age of complete maturity for females (AM_{95}) ranged from 7.7 years to 21.1 years. Complete maturity for males ranged from 7.5 to 20.1 years. Ages at which males and females were all mature were similar for each population except for Twobit Lake where males matured at a younger age.

Estimates of the length at which 50% of the female lake trout from these populations matured (LM_{50}) varied from 348 to 481 mm. The range of values for LM_{50} were relatively less than for AM_{50} (Figure 3). The coefficient of variation between the estimates of LM_{50} was 10.8 percent (sd, 44.1) compared with 29.5% (sd, 2.6) for estimates of AM_{50} . In general, the estimates of LM_{50} for females were not different between the populations studied. Lack of overlap in the 95% fiducial limits for the estimates indicates the LM_{50} for females from four of the largest lakes (Walker Lake, Fielding, Summit,

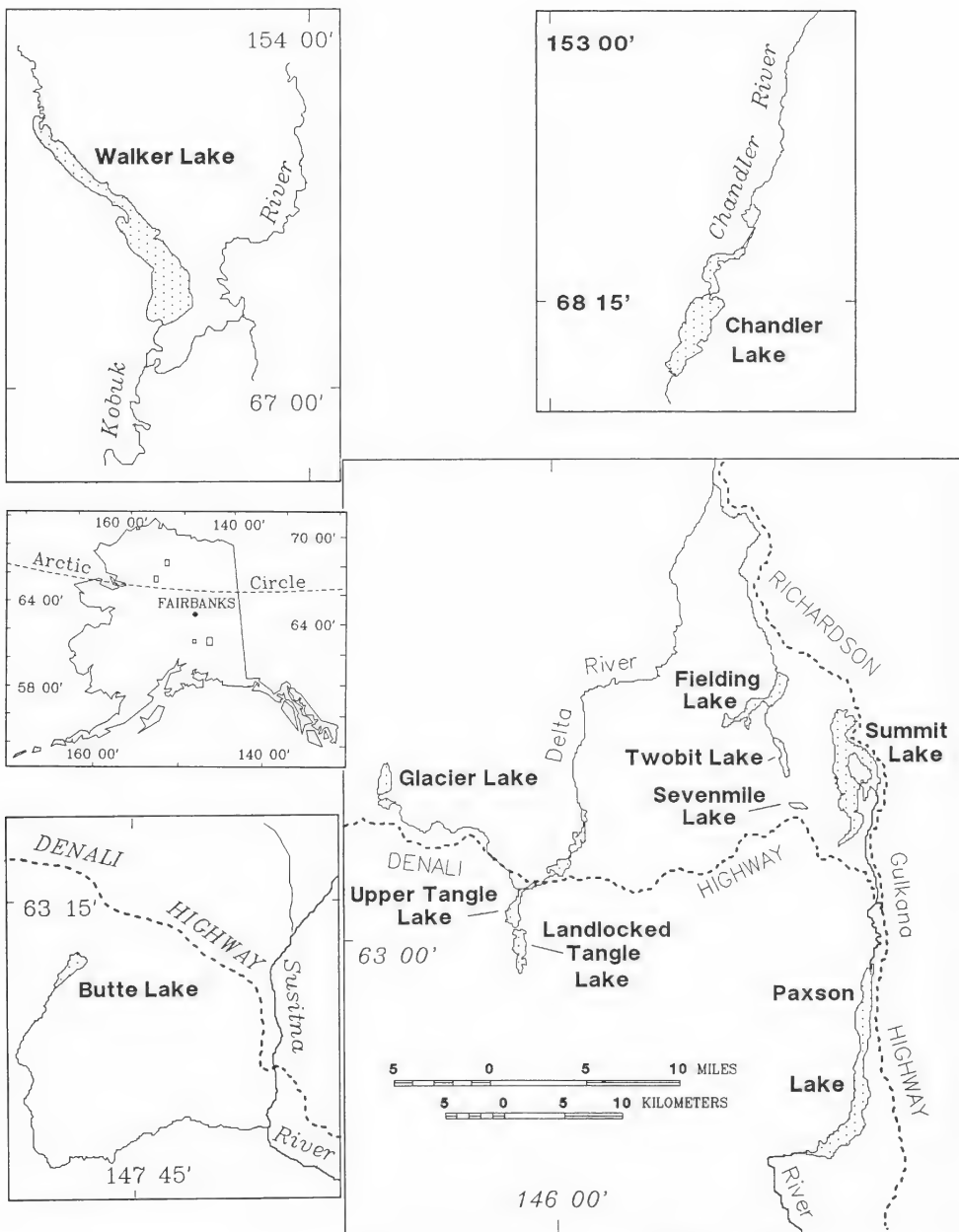


Figure 1. Study lakes in Alaska Mountain Range and in the Brooks Mountain Range.

TABLE 1. Location, elevation, surface area, maximum depth and fish species in the 11 study lakes.¹

Lake	Location	Elevation (m)	Area (ha)	Maximum Depth (m)	Fish Species ² Present
Sevenmile	63° 06' N 145° 37' W	925	33	12	BB,SC,LT
Paxson	62° 55' N 145° 33' W	778	1,575	26	BB,GR,HW,RW,SC,SS,LT
Summit	63° 08' N 145° 33' W	978	1,650	70	BB,GR,RW,SC,SS,LT
Fielding	63° 10' N 145° 40' W	906	538	24	BB,GR,RW,SC,LT
Upper Tangle	63° 02' N 146° 03' W	868	150	27	BB,GR,LS,RW,SC,LT
Butte	63° 10' N 147° 50' W	1,022	318	24	GR,RW,SC,LT
Glacier	63° 07' N 146° 15' W	1,124	177	27	BB,GR,RW,SC,LT
Landlocked Tangle	63° 00' N 146° 06' W	872	241	37	BB,GR,RW,SC,LT
Twobit	63° 08' N 145° 38' W	1,006	109	24	SC,LT
Chandler	68° 14' N 152° 44' W	914	1,300	22	AC,BB,GR,RW,SC,LT
Walker	67° 08' N 154° 20' W	206	3,800	122	AC,BB,CS,GR,LC,NP,LT,RW,SC

¹Lakes ordered by increasing mean age to 50% maturity (AM₅₀) of lake trout.

²AC-*Salvelinus alpinus*, BB-*Lota lota*, CS-*Oncorhynchus keta*, GR-*Thymallus arcticus*, LC-*Coregonus sardenella*, LT-*Salvelinus namaycush*, LS-*Catostomus catostomus*, NP-*Esox lucius*, RW-*Prosopium cylindraceum*, SC-*Cotus cognatus*, SS-*Oncorhynchus nerka*.

Paxson) are larger than from most of the smaller lakes (Landlocked Tangle, Twobit, Glacier) but not all (Sevenmile, Butte). In most of the populations, male lake trout appear to mature at a smaller size (335-460 mm) than females. However, differences between males and females were seen only in the samples from Paxson, Summit, and Fielding lakes. The length at first maturity estimated by LM₅ for female lake trout ranged from 266 mm in Twobit Lake to 428 mm in Fielding Lake. No females encountered from any of the lakes were mature at fork lengths less than 290 mm. In most populations, the estimated length of first maturity for males appears to be less than for females but differences in the fiducial intervals were seen only for Paxson and Summit Lakes. Estimates of LM₉₅ for females ranged from 420 mm to 600 mm and for males from 389 mm to 678 mm (Figure 3).

In Sevenmile Lake, all age 4 fish were immature and all age 6 fish were mature. Estimates for maturity were not obtained from the probit procedure due to the "knife-edged" maturity of lake trout in this population. Other methods are recommended for populations with this type of maturation (Trippel and Harvey 1991). First and complete maturity could not be estimated with the probit procedure from samples of either sex from Upper Tangle Lake and for females from Chandler Lakes. The 95% fiducial limit around the estimate of LM₅₀ for males from Walker Lake ranged from 0 to 540

mm and is not shown in Figure 3. Small sample sizes were likely responsible for the failure of probit analysis to accurately predict the length and age of first and complete maturity for these populations (Figure 2, 3).

Discussion

The estimates of first and complete maturity from probit analysis were generally not different from values observed in the samples. The minimum observed values for age and length of first maturity fell within the 95 percent fiducial interval for 5 percent maturity most of the time (87% of the time for age, 88% for length). Similarly, values for complete maturity from the samples were generally within the 95 percent limits of AM₉₅ and LM₉₅ (ages 87.5%, lengths 95%). The point estimates for age and length at first maturity were often less than the youngest or smallest mature fish encountered in the samples. However, actual differences were observed only for males from Paxson and Chandler Lakes. The source of this potential bias is unknown but may be due either to errors in age determination or to incorrectly assigning mature status to immature fish. Similarly, estimates for the age and length at complete maturity predicted with probit analysis were often older and larger than encountered in the samples. Differences between estimated and observed age at complete maturity

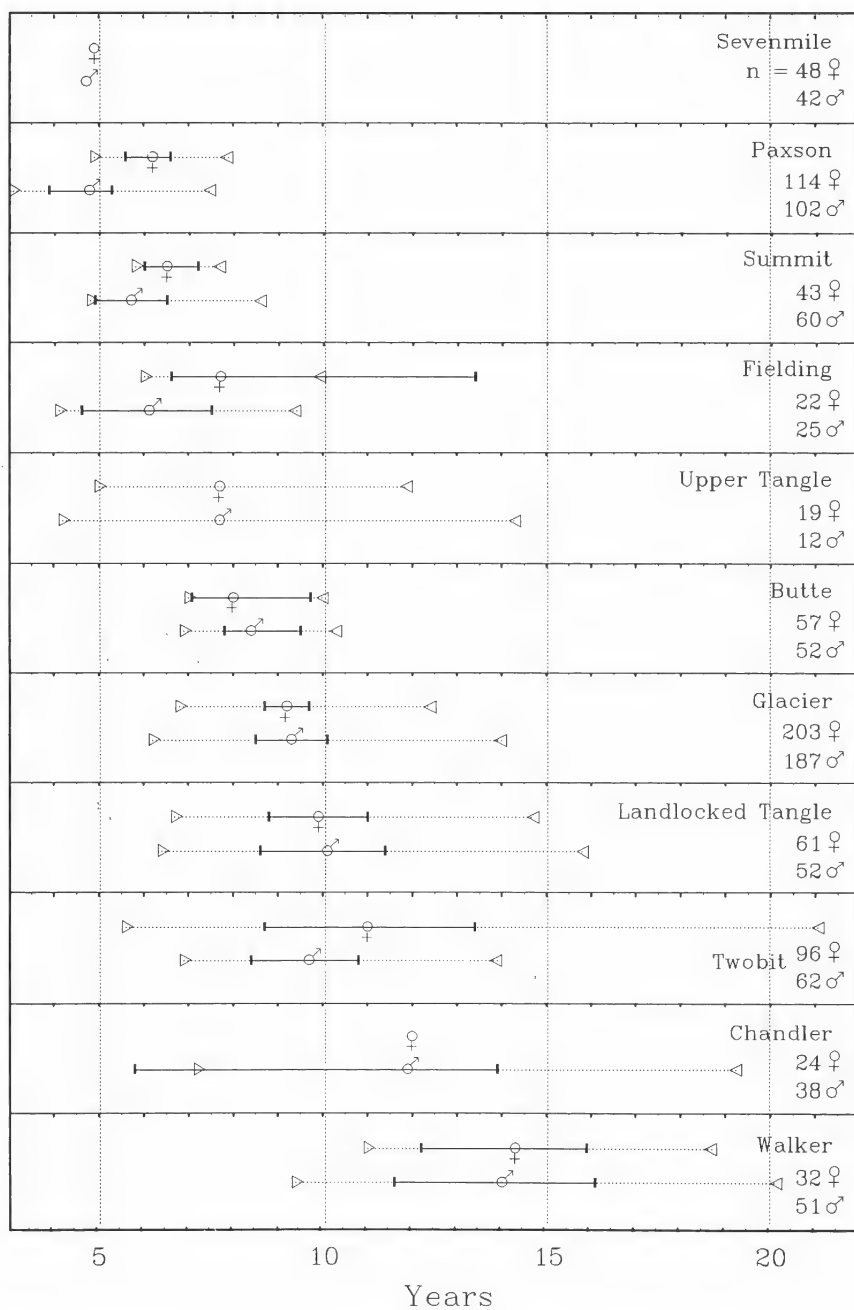


Figure 2. Age at maturity for 11 lake trout populations from Alaska. Age at 50% maturity is shown by sex symbol, fiducial limits around estimate are shown by solid bar. Ages at first and complete maturity are shown by open triangles and connected by broken line.

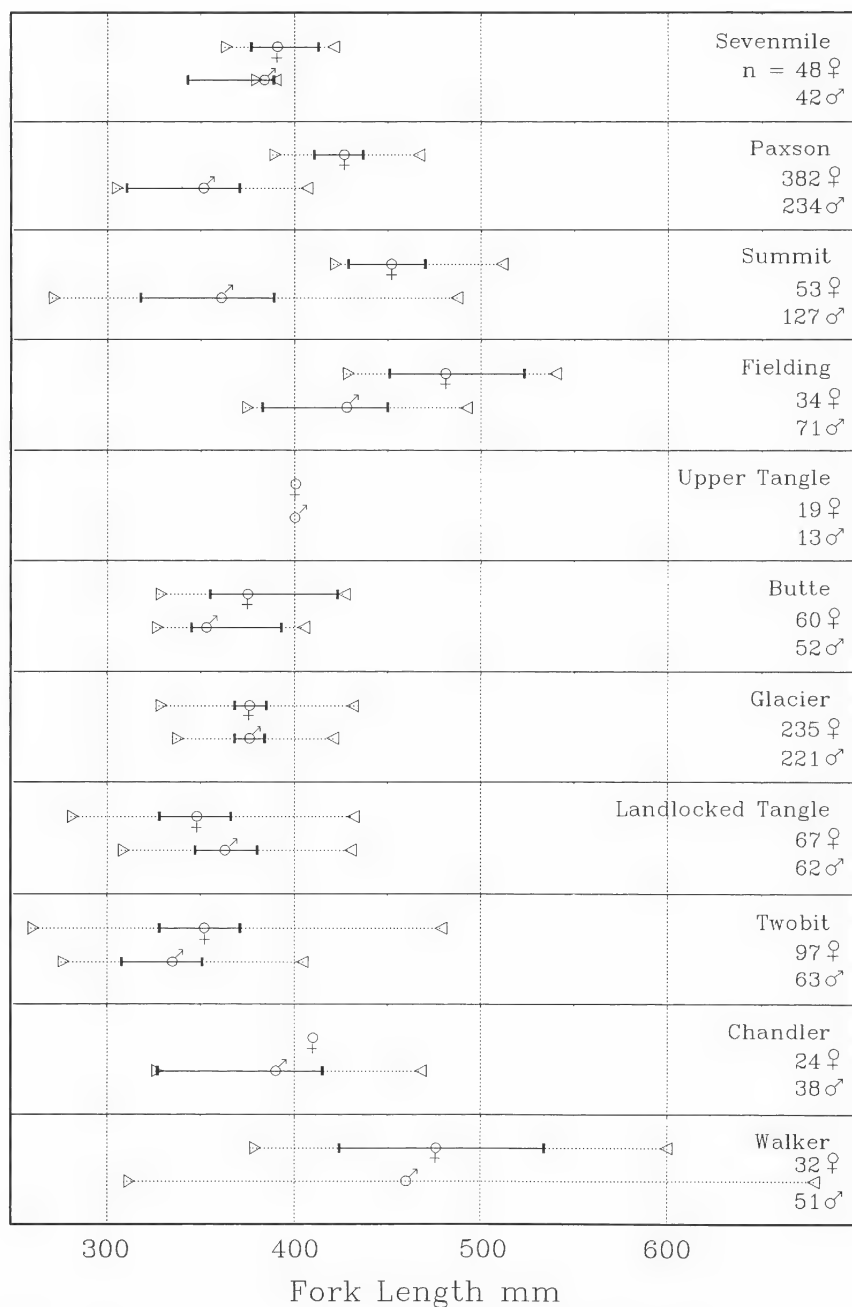


Figure 3. Length at maturity for 11 lake trout populations from Alaska. Length at 50% maturity is shown by sex symbol, fiducial limits around estimate are shown by solid bar. Lengths at first and complete maturity are shown by open triangles and connected by broken line.

were detected only for males from Chandler and Walker Lakes and for length at complete maturity only for males from Walker Lake. Failure to recognize as mature males that would not have spawned in the year of capture but that had spawned previously may be one source of this potential bias. Non-consecutive spawning is common in northern populations (Martin and Olver 1980).

Estimates of the median age at maturity from the 11 Alaskan lake trout populations in the study (5-14 years) are within the range reported for the species (Healey 1978, Martin and Olver 1980, Donald and Alger 1986, Table 2). Length at maturity for lake trout populations in Alaska (335-481 mm) are generally less than those observed for populations farther south, but are within the range reported (Table 2). Differences in the rate of maturation in lake trout have been related to a number of environmental and biological factors such as latitude, altitude, growth, lake size, and available forage. Maturity is often related to the attainment of a given size and age such that fast growing lake trout may mature at an earlier age and the largest members of an age group are the first to mature (Martin and Olver 1980). For lake trout, the lower limit of age of maturity appears to be 4 years and at a length of approximately 200 mm (Table 2).

Maturity is expected to be slower in populations in high latitude and altitude lakes due to low available solar energy (Henderson *et al.* 1973) and slow growth (Healey 1978). In this study, estimates of median age at maturity were highest (12 and 14 years) for the two populations north of 67° latitude (Walker and Chandler Lakes). Reports of median age at maturity from high latitude populations in Alaska (Itkillik, Campsite, and Old John Lakes) and from northern Canada (e.g., Great Bear Lake, and Kaminurik Lake, Table 2) are similar to results found at Walker and Chandler Lakes. In contrast, estimates of age at maturity from the nine lake trout populations investigated farther south (62° 55' to 63° 10' N) are consistently younger (AM₅₀ 5.4-10.4 yrs) than estimates from populations residing in lakes at higher latitudes. The age at maturity for lake trout in these lower latitude Alaskan lakes are similar to results from Lake Tahoe in California and more temperate areas in Canada (Table 2). An increase in age of maturity with increase in latitude was reported by Falk *et al.* (1973) and Healey (1978). Length at maturity may also decrease with increasing latitude (Healey 1978). In this study, latitude is not inversely related

to LM₅₀. The effect of elevation on length or age at maturity was not evident in the Alaskan lakes, but the range of elevation in this study was quite limited (Table 1).

Differences in age at maturity among populations have been attributed to differences in growth rates such that age and size of maturity are inversely related (Alm 1959, Hanson and Wickwire 1967, Paterson 1968). In contrast, Healey (1978) found that size and age at maturity were not correlated. In some populations (primarily planktivorous) small fish mature at young age (Martin 1966, Donald and Alger 1986). An inverse relationship between age and length at maturity between populations was not observed in the results from the 11 Alaskan populations (Figures 2, 3).

Lake size may also affect the length at which lake trout mature. Lake area is highly correlated with measures of community structure, catch and harvest, and numerous abiotic factors (Goddard *et al.* 1987). A significant correlation between lake area and LM₅₀ for lake trout, and a positive relation between area and L_{infinity} is reported by Payne *et al.* (1990). This means larger lakes contain populations with larger lake trout and correspondingly greater LM₅₀. In Alaska, length at 50% maturity for females was generally larger in the larger lakes; all estimates greater than 400 mm were from lakes larger than 500 ha. The overall smaller size at maturity for lake trout from lakes in the Alaska Range is likely a result of the small surface area of these lakes. Most lakes that have been studied in areas outside Alaska are relatively larger; Sas-senach Lake, Alberta is smaller (8.1 ha), length at maturity is less (Donald and Alger 1986).

The effect that lake surface area has on the size at maturity for lake trout is significant in consideration of length limit regulations. The median lengths at maturity estimated as LM₅₀ for the lakes in Alaska, indicate that the 420 mm FL length limit adopted in Alaska is unlikely to provide protection for first spawning lake trout in lakes larger than 500 ha (Figure 2). For lakes 320 ha and smaller in this study, the estimated median length at maturity was less than the length limit, and protection for lake trout through first spawning can be expected.

Available forage and diet may also affect the age and size of maturity for lake trout. Small lakes in Alaska are inhabited by few fish species (Table 1). In other studies, slow-growing lake trout which feed on plankton matured earlier than fast-growing

TABLE 2. Maturity schedules for lake trout from selected North American populations¹

Lake	Fork Length at maturity			Age at maturity			Reference
	1st mature	50% mature	All mature	1st mature	50% mature	All mature	
Tahoe, Calif-Nev	335 m ² 422 f	505 m 531 f	610 m 620 f	4 m 4 f	7 m 8 f	10 m 11 f	Hanson & Wickwire 1967
Louisa, Ontario	330 f	355 f	400 f	6 f	7 f	8 f	
Algonquin Park, Ont	250 m 330 f			4 m 5 f	6 b		Martin 1951, 1956 Martin 1957, 1966
Opeongo, Ontario	380 f	457-500 f	480-580 f				
Squeers, Ontario		310 m	395 m	5 m	7 m	9-11 m	Martin & Fry 1973 Ball 1988
	280 f	366 f	415 f	7 f	8 f	9-11 f	
Mistassini, Quebec				7 m		9 m	Dubois & Lageux 1968
	483 f	511 f		9 f	11 f		
Swan, Alberta				5 m			Paterson 1968
	479 f	479 f	525 f	6 f	6 f	7 f	
Sassenach, Alberta	180 m 200 f	180 m 220 f	200 m	4 m 6 f	4 m 7 f	5 m	Donald & Alger 1986
la Ronge, Sask	500 f	560 f	612 f	5 f	7 f	8 f	
Great Slave, N.W.T.	484 b			8-9 f	8-10 f	14-19 f	Rawson 1961 Falk <i>et al.</i> 1974
Paxson, Alaska			450 b			7-9 b	
Paxson	304 m 388 f	351 m 426 f	405 m 467 f	3 m 5 f	5 m 6 f	8 m 8 f	Van Whye & Peck 1968 This study
Kaminuriak, N.W.T.				13 m			
	545 f	610 f		19 f	27 f		Bond 1975
Hottah, N.W.T.	465 f	465 f	526 f	5 b	5 b	7 f	
Landlocked Tangle	308 m 281 f	363 m 348 f	429 m 431 f	6 m 7 f	10 m 10 f	16 m 15 f	Wong & Whillans 1973 This study
Upper Tangle		400 m		4 m	8 m	14 m	
		400 f		5 f	8 f	12 f	This study
Sevenmile	379 m 363 f	348 m 391 f	389 m 420 f		5 m 5 f		
Glacier	337 m 328 f	376 m 376 f	421 m 432 f	6 m 7 f	9 m 9 f	14 m 12 f	This study
Twobit	315 m 327 f	335 m 352 f	405 m 479 f	7 m 7 f	10 m 11 f	14 m 22 f	
Summit, Alaska			500 b			8-10 b	Van Whye & Peck 1968 This study
Summit	271 m 421 f	361 m 452 f	487 m 511 f	4 m 6 f	6 m 7 f	9 m 8 f	
Butte	326 m 328 f	353 m 375 f	405 m 427 f	7 m f	8 m 8 f	10 m f	This study
Fielding	374 m 428 f	428 m 481 f	491 m 540 f	4 m 6 f	6 m 8 f	9 m 10 f	
Keller, N.W.T.	500 b			11 f			Johnson 1972 Falk <i>et al.</i> 1974
Great Bear, N.W.T.	448 b				14 m		
				10-11 f	14-15 f	15-20 f	This study
Walker	311 m 378 f	460 m 476 f	678 m 600 f	9 m 11 f	14 m 14 f	20 m 19 f	
Old John, Alaska	350 b		450 b	10 b		15 b	Craig & Bain 1975 This study
Chandler	326 m 410 f	390 m	468 m 425 f	7 m	12 m 12 f	19 m	
Itkillik, Alaska	400 m 450 f		450 m	11 m 14 f	11-15 m 15-17 f	17 m 20 f	McCart <i>et al.</i> 1972
Campsite, Alaska		350 m 350-400 f			11 m 13 f		

¹Lakes ordered by increasing latitude.²m—males, f—females, b—both sexes

piscivorous lake trout, and a change in diet from plankton to fish resulted in an increase in size and age of maturity (Martin 1966). The absence or unavailability of suitable-sized forage fish for lake trout resulted in a diet of benthic invertebrates, smaller fish (including lake trout), and plankton in many northern populations (Falk *et al.* 1973, Ball 1989). Such populations may become dominated by small, slow-growing or "stunted" individuals (Donald and Alger 1986, Carl *et al.* 1990). In contrast to the slow growing, early maturing, planktivorous lake trout described by Martin (1966), lake trout in Alaskan lakes with limited forage mature at small size and old age. Twobit Lake in Alaska has the lowest fish species diversity in the data set, and estimates of AM₅₀ (11 yrs) and LM₅₀ (352 mm) for female lake trout from Twobit Lake

are older and smaller than for other populations in the Alaska Mountain Range. Alaskan lake trout populations in smaller lakes are generally benthivorous/planktivorous and species diversity and piscivory increases with lake size.

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Literature Cited

- Alm, C. 1959. Connection between maturity, size, and age in fishes. *Inst. Freshwat. Res. Drottningholm* 40:123-137.
- Carl, L., M.-F. Bernier, W. Christie, L. Deacon, P. Hulsman, D. Loftus, D. Maraldo, T. Marshall, and P. Ryan. 1990. Fish community and environmental effects on lake trout. Lake trout synthesis, Ontario. Min. Nat. Resour., Toronto. 47 p.
- Craig, P. C., and J. Wells. 1975. Fisheries investigations in the Chandalar River region, northeast Alaska. Canadian Arctic Gas Study Limited (Calgary, Alberta), Biological Report Series. 105 p.
- Donald, D. B., and D. J. Alger. 1986. Stunted lake trout from the Rocky Mountains. *Can. J. Fish. Aquat. Sci.* 43:608-612.
- Eschmeyer, P. H. 1955. The reproduction of lake trout in southern Lake Superior. *Trans. Amer. Fish. Soc.* 84:47-74.
- Falk, M. R., D. V. Gilman, and L. W. Dahle. 1973. The 1972 sports fisheries of Great Bear and Great Slave lakes, Northwest Territories. *Fish. Mar. Serv. Rep. Ser. CEN/T-73-8*: 100 p.
- Finney, D. J. 1971. Statistical methods in biological analysis, 2nd ed. Charles Griffin & Company, Ltd., London. 668 p.
- Goddard, C. I., D. H. Loftus, J. A. MacLean, C. H. Olver, and B. J. Shuter. 1987. Evaluation of the effects of fish community structure on observed yields of lake trout (*Salvelinus namaycush*). *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2):239-248.
- Hanson, J. A., and R. H. Wickwire. 1967. Fecundity and age at maturity of lake trout, *Salvelinus namaycush*, in Lake Tahoe. *Calif. Fish Game* 53:154-164.
- Healey, M. C. 1978. Dynamics of exploited lake trout populations and implications for management. *J. Wildlife Mgmt.* 42:307-328.
- Henderson, H. F., R. A. Ryder, and A. W. Kudhognia. 1973. Assessing fishery potential of lakes and reservoirs. *J. Fish. Res. Bd. Can.* 30(12/2):2000-2009.
- MacCrimmon, H. R., and E. Skobe. 1970. The fisheries of Lake Simcoe. Ont. Dep. Lands and Forests, Fish Wildlife Branch. Toronto. 140 p.
- Martin, N. V. 1952. A study of the lake trout, *Salvelinus namaycush*, in two Algonquin Park lakes. *Trans. Amer. Fish. Soc.* 81:111-137.
- . 1966. The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. *Trans. Amer. Fish. Soc.* 95:415-422.
- Martin, N. V. and C. H. Olver. 1980. The lake charr, *Salvelinus namaycush*. In E. K. Balon, ed. "Charrs: Salmonid fishes of the genus *Salvelinus*." D. W. Junk, Publishers, The Hague, Netherlands. 925 p.
- Miller, R. B., and W. A. Kennedy. 1948. Observations on the lake trout of Great Bear Lake. *J. Fish. Res. Board Can.* 7:176-189.
- McCart, P., P. Craig, and H. Bain. 1972. Report on fisheries investigations in the Sagavanirktok River and neighboring drainages. Report to Alyeska Pipeline Service Company, Bellevue, Wash. 170 p.
- Nordeng, H. 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, north Norway. I. Age and spawning frequency determined from scales and otoliths. *Nytt. Mag. Zool.* 10:67-123.
- Paterson, R. J. 1968. The lake trout (*Salvelinus namaycush*) of Swan Lake, Alberta. Alberta Department of Land Forests. Fish and Wildlife Division of Research Report 2:1-149.
- Payne, N. R., R. M. Korver, D. S. MacLennan, S. J. Nepszy, B. J. Shuter, T. J. Stewart, and E. R. Thomas. 1990. The harvest potential and dynamics of lake trout populations in Ontario. Lake trout synthesis, Ont. Min. Nat. Resour. Toronto. 72 p.
- Olver, C. H., and C. A. Lewis. 1977. Reproduction of planted lake trout, *Salvelinus namaycush*, in Gamitagama, a small Precambrian lake in Ontario. *J. Fish. Res. Board Can.* 34:1419-1422.

- Royce, W. F. 1943. The reproduction and studies on the life history of the lake trout, *Cristivomer namaycush* (Walbaum). Ph.D. Thesis, Cornell Univ., Ithaca, N.Y. 136 p.
- Sharp, D., and D. R. Bernard. 1988. Precision of estimated ages of lake trout (*Salvelinus namaycush*) from five structures. N. Amer. J. Fish. Mgmt. 8:367-372.
- Surber, T. 1933. Rearing lake trout to maturity. Trans. Amer. Fish. Soc. 63:64-68.
- Trippel, E. A., and H. H. Harvey. 1991. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). Can. J. Fish. Aquat. Sci. 48:1446-1459.
- Van Whye, G. L., and J. W. Peck. 1968. A limnological survey of Paxson and Summit lakes in interior Alaska. Alaska Dept. Fish & Game Inf. Leaflet. 124:1-39.

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Gregory A. Green,¹ Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, Oregon 97331

Richard E. Fitzner,² Battelle, Pacific Northwest Laboratories, P.O. Box 999, Richland, Washington 99352

Robert G. Anthony, U.S. Fish and Wildlife Service, Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, Oregon 97331

and

Lee E. Rogers, Battelle, Pacific Northwest Laboratories, P.O. Box 999, Richland, Washington 99352

Comparative Diets of Burrowing Owls in Oregon and Washington

Abstract

We studied diets of breeding burrowing owls (*Speotyto cunicularia*) in the Columbia Basin of southcentral Washington and northcentral Oregon during 1977-78 and 1980-81, respectively. Vertebrates, primarily rodents, comprised only 9.6 percent of the total prey numbers contained in 6,328 regurgitated pellets but 87.3 percent of the biomass in the two samples combined. Vertebrate prey use was twice as high in Washington (17.1%) as in Oregon (8.4%). We attributed this to differences in habitat, including soil type, and the effects of annual variations in rainfall on prey populations. Great Basin pocket mice (*Perognathus parvus*) dominated the vertebrate prey in both states and contributed the greatest overall biomass (35.0%). Orthopteran insects comprised the greatest invertebrate biomass (10.2%), while three families of beetles contributed 49.0 percent of the total individual prey, but only 1.3 percent of the biomass. Soil type influenced differences in vertebrate composition in Oregon. Mean dry mass of over 76 prey taxa ranged from <4 mg to >40 g, indicating this species has a broad range of prey size.

Introduction

Knowledge of a raptor's diet is an important component of an effective management plan. Because all raptors are carnivorous, management objectives should consider the prey base. However, raptor diets are often site-specific and contingent upon regional availability of potential prey (Jaksic and Marti 1981). Therefore, locally collected data can be misleading when applied to another site or general region. This is especially true for generalists with a broad foraging niche. Consequently, diet data should be collected locally to insure an accurate assessment of forage use and then compared to other regions to determine the uniqueness of the local diet.

Prey availability can also change within a region on an annual basis as the prey base is influenced by changing factors such as weather, population dynamics, vegetation growth, and human activities (especially agriculture). Therefore, data collected for only one year may provide a misleading view of raptor food habits and a misleading view of the region's potential prey base. Consequently, data should be collected for more than one year to assess annual variation.

We report on the diet of breeding burrowing owls (*Speotyto cunicularia*) in shrub-steppe habitats at two locations in the Columbia Basin from data collected over separate two-year periods. We compare our results among years, locations, and soil types within our study area to better quantify spatial and temporal variations in the owl's diet. We also compare our results with data collected from other large ecosystems (Colorado, California, and Chile) to gain a better perspective on the regional trophic ecology of the Columbia Basin relative to burrowing owl food habits.

Study Area and Methods

The studies were conducted in the shrub-steppe zone of northern Gilliam, Morrow, and Umatilla counties in northcentral Oregon and at the U.S. Department of Energy's (DOE) Hanford Site in north Benton County, southcentral Washington. The topography in both study areas ranges from flat to undulating, with elevations ranging from 75 m to 200 m. The average annual precipitation for both study areas is approximately 22 cm (Ruffner 1978), most of which falls during the winter and early spring. Summers are hot and dry with several days of maximum temperatures exceeding 40°C.

The natural vegetation of the study areas is included in the *Artemisia/Stipa* or *Artemisia/Roegneria* [= *Agropyron*] plant associations (Poulton

¹Present address: Ebasco Environmental, 10900 N.E. 8th, Bellevue, Washington 98004-4405.

²Deceased.

1955), but climax vegetation is rare because of edaphic conditions, fire, or livestock grazing. Cheatgrass (*Bromus tectorum*) is a major alien invader and dominates much of the study areas. Less disturbed grasslands were dominated by western needle-and-thread (*Stipa comata*) at the lower elevations (<100 m) and bluebunch wheatgrass (*Roegneria spicata* [= *Agropyron spicatum*]) at the higher elevations (>100 m). Important shrubs in both study sites included big sagebrush (*Artemisia tridentata*), antelope bitterbrush (*Purshia tridentata*), gray rabbitbrush (*Chrysothamnus nauseosus*), and snakeweed (*Gutierrezia sarothrae*). Burrowing owl nest sites were found in cheatgrass-dominated grasslands, snakeweed shrublands, or sparse shrublands of tall sagebrush or bitterbrush which was associated with cheatgrass or sparse bluebunch wheatgrass.

Diets of burrowing owls were determined by analyzing regurgitated pellets. Pellets were collected from around each nest site and at nearby perches every 1-3 weeks during the nesting season (April-July) and soaked overnight in a 2-molar (8%) solution of NaOH (Degn 1978) to dissolve hair. After material was strained and dried, vertebrate and arthropod parts were separated from the pellet mass, identified to the lowest taxon possible, and the number of individuals counted. Head capsules, elytra, and jaws of arthropods, and skulls and dentaries of vertebrates were the main body parts used in identification. Fragments were identified by comparing to specimens in museum collections at Oregon State University and Battelle PNW Laboratories. All data were converted to biomass (dry weight) from Rogers *et al.* (1976), Gleason and Craig (1979), and specimens collected at the study sites.

Results and Discussion

We collected and analyzed a total of 6,328 pellets of which 769 were collected from 5 nest sites at the Washington site in 1977-78 and 5,559 from 65 nests at the Oregon study area in 1980-81. These samples comprised a total of 37,431 individual prey representing 35,269 g (dry) of biomass and included 14 species of small mammals, 3 species of birds, 2 reptiles, 1 amphibian, and at least 56 species of arthropods. Estimated biomass of each taxon ranged from 4 mg to 41.6 g. For both study sites and all years combined, arthropods made up 90.4 percent of the prey individuals

but only 12.7 percent of the biomass, while small vertebrates, mostly rodents, comprised the balance (Table 1).

A higher percentage of vertebrate prey numbers was found in diets in Washington (17.1%) than from Oregon (8.4%), which may have been a result of a higher availability of Orthoptera (Acrididae, Tettigonidae, and Gryllacrididae) prey at the Oregon study site. Grasshoppers, especially *Melanoplus* sp., were at or near epidemic proportions both years of the Oregon study and were preyed upon heavily by the owls probably to the near exclusion of other prey by late summer. Four species of small mammals were common among the vertebrate prey in Washington and six species in Oregon. Great Basin pocket mice (*Perognathus parvus*) dominated the vertebrate prey in both areas and contributed 35 percent of the total biomass. Other studies (O'Farrell *et al.* 1975, Green 1983) have found pocket mice at greater densities than all other small rodents on both areas. Differences in small mammal prey composition between the two areas reflected differences in prey species ranges and habitat types. Ord's kangaroo rat (*Dipodomys ordii*) does not occur on the Washington study area and consequently was found only in the Oregon owl diets. The sagebrush vole (*Lagurus curtatus*) was found in burrowing owl diets only on the loamy-soils in Washington, while montane voles (*Microtus montanus*) were found only in the diets of Oregon owls. These differences probably reflect habitat rather than range differences. The largest vertebrate prey were neonate Nuttall's cottontails (*Sylvilagus nuttallii*) and black-tailed jackrabbits (*Lepus californicus*) which together contributed >10 percent of the biomass in Oregon. Northern pocket gophers (*Thomomys talpoides*) in the diets were generally juveniles.

The most common insect prey were the tenebrionid beetles *Conisattus nelsoni* (Washington) and *Blapstinus* sp. (Oregon) and the scarab beetle *Diplotaxis subangulata* (Oregon). These three species alone contributed over 28 percent of the total individuals. All three species are small (<7 mg) and contributed <0.3 percent of the total biomass. Active pursuit of these insects by burrowing owls may result in a negative energy gain to the owls, especially since adult burrowing owls carry single prey to their young. Owls were foraging primarily for their young during our study. We speculate that the adults and perhaps nestlings were passively feeding on these insects within the nest and roost

TABLE 1. Diet composition of burrowing owls in the Columbia Basin of southcentral Washington (1977-78) and northcentral Oregon (1980-81).

Prey	Washington		Oregon		Total		Total No.
	(n=769 pellets)		(n=5,559 pellets)		(n=6,328 pellets)		
	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass	
Vertebrates	(17.1)	(89.9)	(8.4)	(86.7)	(9.6)	(87.3)	(3,592)
<i>Sylvilagus nuttallii</i>	<0.1	1.9	0.2	10.0	0.2	8.5	72
<i>Thomomys talpoides</i>	1.1	19.8	0.7	20.4	0.8	20.3	286
<i>Perognathus parvus</i>	10.5	44.9	5.1	32.7	5.8	35.0	2,167
<i>Dipodomys ordii</i>	0.0	0.0	0.4	8.7	0.4	7.1	136
<i>Peromyscus maniculatus</i>	1.6	6.2	1.6	9.8	1.6	9.1	604
<i>Lagurus curtatus</i>	1.4	6.1	0.0	0.0	0.2	1.2	69
<i>Microtus montanus</i>	0.0	0.0	0.3	4.6	0.3	3.8	105
Other vertebrates	2.5	11.1	0.1	0.5	0.3	2.5	153
Invertebrates	(82.9)	(10.1)	(91.6)	(3.3)	(90.4)	(12.7)	(33,839)
Scorpionida	3.7	1.0	0.5	0.2	1.0	0.4	360
Solpugida	1.0	0.1	0.5	<0.1	0.5	<0.1	201
Araneida	2.7	0.1	0.0	0.0	0.4	<0.1	137
Acrididae	0.8	0.1	8.7	2.5	7.6	2.0	2,856
Tettigonidae	8.5	6.5	12.1	3.3	11.6	3.9	4,345
Gryllacrididae	6.3	0.8	13.0	5.2	12.1	4.3	4,538
Carabidae	9.2	0.2	9.8	0.2	9.7	0.2	3,644
Silphidae	4.5	0.5	4.3	0.7	4.3	0.7	1,623
Scarabacidae	14.2	0.4	14.5	0.3	14.5	0.4	5,422
Tenebrionidae	27.5	0.4	24.3	0.8	24.8	0.7	9,269
Other invertebrates	4.5	<0.1	3.9	0.1	3.9	0.1	1,456
Total numbers and estimated biomass (g)	5,031	6,685	32,400	28,584	37,431	35,269	37,431

burrows. In support of this, over 80 hr of feeding observations by the senior author failed to note any direct feeding on these insects. The beetles are probably attracted to the cool moist burrows and nest litter contained within.

Large Orthoptera were the only invertebrates of which individual taxa contributed >1 percent of the total biomass. In Washington, the coulee cricket (*Apote notabilis*) was by far the most important invertebrate prey, contributing 6.5 percent of the biomass. Coulee crickets were also the largest insect prey averaging over 1 g (dry weight). The most important invertebrate prey in Oregon was the Jerusalem cricket (*Stenopelmatus fuscus*—5.2% of the biomass) followed by the migratory grasshopper (*Melanoplus sanguinipes*—2.5%), the coulee cricket (1.7%), and *Steiraxys* sp. (1.7%). Jerusalem crickets (*Stenopelmatus* spp.) have been reported to be important in the diet of other burrowing owl populations (Maser *et al.* 1971, Thomsen 1971, Gleason and Craig 1979, Brown *et al.* 1986). Other important invertebrate prey in-

cluded the burying beetle (Silphidae; *Nicrophorus* sp.—0.7% of the total biomass), several species of darkling beetles (Tenebrionidae; *Eleodes* spp.—0.6%), and scorpions (0.4%). Overall, the insect families Carabidae, Scarabacidae, and Tenebrionidae contributed over 30 prey species and 49 percent of the individuals consumed but only 1.3 percent of the total biomass.

Diets of burrowing owls elsewhere (reviewed by Gleason and Craig [1979]) have shown, as in this study, that these raptors feed predominantly on arthropods and small mammals. Our overall vertebrate:arthropod ratio (10:90%) is very similar to Marti's (1974) results (8:92%) from Colorado; however, prey species composition was quite different. Much higher percentages of vertebrates were found in burrowing owl diets in California (29.3%, Jaksic and Marti 1981; 31.4-41.2%, Thomsen 1971) and Chile (20.0%, Jaksic and Marti 1981). Jaksic and Marti (1981) surmised that the greater proportion of vertebrate prey at their California and Chile study sites

compared to the Colorado site reflected differential prey availability rather than differential selection.

We too attribute the differences between Oregon and Washington owl diets to differential prey availability, which in turn are affected by habitat differences (including soil type), annual variations in rainfall on summer estivation patterns of rodents, and the annual variation of insect populations. For instance, at the Oregon site in 1980, vertebrates comprised 12.6 percent of the diet even though grasshoppers (Acrididae—26.4%) were at epidemic population levels and the proportion of vertebrates in the diet had dramatically decreased from 49 percent in April to less than 5 percent in August (Green and Anthony 1989). In contrast, the composition of vertebrates and grasshoppers in the Oregon diet in 1981 decreased to 7.0 percent and 2.8 percent, respectively, with a corresponding increase in coleopteran prey from 23.3 percent to 62.7 percent; suggesting significant annual variations in diet. Furthermore, O'Farrell *et al.* (1975) determined that annual rainfall in the Columbia Basin and its effect on seed production governed the density and aboveground activity of Great Basin pocket mice. In their study, pocket mice had five-fold changes in population size and 30-day differences in above-ground activity between wet and dry years. Because the Oregon and Washington studies were not conducted during the same years, annual variation in rainfall may have contributed to differences in diet composition.

In addition, differences in vertebrate prey composition between Washington and Oregon were influenced by differences in soil type. Edaphic factors such as depth, texture, and strength have been found to affect populations of small mammals (Best 1969, Kritzman 1974, Feldhammer 1979). Within the Washington and Oregon study sites, two basic soil types were present, loamy-sand and silty-loam. Within the loamy-sand sites pocket mice clearly dominated both the percent number and percent biomass of the mammalian prey at both sites (Table 2). While at the silty-loam sites in Oregon, deer mice (*P. maniculatus*), northern pocket gophers, and Great Basin pocket mice were found in nearly equal numbers, but pocket gophers provided most of the biomass (Table 2). In Washington, pocket gophers also dominated the biomass on silty-loam sites, although pocket mice represented 36 percent of the biomass. In terms of numbers at the Washington silty-loam sites,

pocket mice and sagebrush voles were most common. Consequently, dietary composition between Oregon and Washington at the loamy-sand sites were very similar, while at the silty-loam sites the dominance of deer mice in Oregon was replaced by sagebrush voles in Washington. Because sagebrush voles occur in the Columbia Basin of Oregon, their absences in the Oregon diets may be a result of habitat differences other than soil types between the Oregon and Washington sites.

TABLE 2. Composition of mammalian prey of burrowing owls nesting in loamy-sand and silty-loam soils in the Columbia Basin of Washington (1977-78) and Oregon (1980-81).

Prey Species	Loamy-sand Soil		Silty-loam Soil	
	% No.	% Biomass	% No.	% Biomass
Washington (n=333)				
<i>Perognathus parvus</i>	80.2	77.2	44.7	36.0
<i>Peromyscus maniculatus</i>	15.6	12.2	5.0	3.2
<i>Thomomys talpoides</i>	1.6	9.0	9.2	44.4
<i>Lagurus curtatus</i>	1.6	0.7	41.1	16.4
Other	1.0	0.9	0	0
Oregon (n=2,689)				
<i>Perognathus parvus</i>	66.4	41.1	26.4	10.5
<i>Peromyscus maniculatus</i>	16.6	11.7	31.1	14.0
<i>Thomomys talpoides</i>	5.0	15.5	28.8	57.1
<i>Dipodomys ordii</i>	4.7	10.7	6.1	8.9
<i>Microtus montanus</i>	3.9	6.2	4.0	4.0
Lagomorphs	2.8	14.5	1.3	4.0
Other	0.6	0.4	2.3	1.5

Feldhammer (1979) found a positive correlation between population densities of Great Basin pocket mice and the percentage of sand in the soil, which may aid their digging efforts, and a negative correlation between percent sand and deer mice densities and speculated that deer mice were avoiding the more arid, sandy soils. The same may be true for northern pocket gophers, although Miller (1964) found that this species occupied the widest range of soil types of the four species of pocket gophers he studied in Colorado.

The shift from vertebrate to orthopteran prey in 1980 and the subsequent shift to coleopteran prey by 1981 in Oregon indicates an opportunistic foraging behavior by burrowing owls. The presence

of a wide variety of prey taxa and sizes, including ichneumon wasps, blow fly pupae, juvenile muskrats (*Odonatra zibethicus*), and crayfish (*Pacifastacus* sp.) further exemplifies opportunistic foraging. The vast difference in mean prey size (<4 mg to >40 g) and the presence of items killed but not eaten (Great Basin spadefoot toad, [*Scaphiopus intermontanus*]) suggests burrowing owls will pursue any potential prey they can physically handle. Schlatter *et al.* (1980) drew the same conclusion based on their study of burrowing owl diets in central Chile.

Over 90 percent of the vertebrate prey and the major insects such as the Jerusalem cricket and burying beetle were nocturnal species. Their presence in the diet indicates that burrowing owls feed nocturnally. Studies by the senior author also revealed intense feeding activity during the crepuscular hours for predominantly ground-dwelling beetles and grasshoppers; little direct feeding activity was observed during the daylight hours.

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Literature Cited

- Best, R. 1969. Habitat, annual cycle, and food of burrowing owls in southwestern New Mexico. M.S. Thesis, New Mexico State Univ., Las Cruces. 34 p.
- Brown, B. A., J. O. Whitaker, T. W. French, and C. Maser. 1986. Note on the food habits of the screech owl and burrowing owl of southeastern Oregon. *Great Basin Nat.* 46:421-426.
- Degn, H. J. 1978. A new method of analyzing pellets from owls, etc. *Dansk. Orn. Foren. Tidsskr.* 72:143.
- Feldhammer, G. A. 1979. Vegetative and edaphic factors affecting abundance and distribution of small mammals in southeast Oregon. *Great Basin Nat.* 39:207-218.
- Gano, K. A., and W. H. Rickard. 1982. Small mammals of a bitterbrush-cheatgrass community. *Northw. Sci.* 56:1-7.
- Gleason, R. L., and T. H. Craig. 1979. Food habits of burrowing owls in southeastern Idaho. *Great Basin Nat.* 39:274-276.
- Green, G. A. 1983. Ecology of breeding burrowing owls in the Columbia Basin, Oregon. M.S. Thesis, Oregon State University, Corvallis. 51 p.
- Green, G. A., and R. G. Anthony. 1989. Nesting success and habitat relationships of burrowing owls in the Columbia Basin, Oregon. *Condor* 91:347-354.
- Henny, C. J., and L. J. Blus. 1981. Artificial burrows provide new insight into burrowing owls nesting biology. *Raptor Res.* 15:82-85.
- Jaksic, F. M., and C. D. Marti. 1981. Trophic ecology of *Athene* owls in mediterranean-type ecosystems: A comparative analysis. *Can. J. Zool.* 59:2331-2340.
- Kritzman, E. B. 1974. Ecological relationships of *Peromyscus maniculatus* and *Perognathus parvus* in eastern Washington. *J. Mammal.* 55:172-188.
- Marti, C. D. 1974. Feeding ecology of four sympatric owls. *Condor* 76:45-61.
- Maser, C., E. W. Hammer, and S. A. Anderson. 1971. Food habits of the burrowing owl in central Oregon. *Northw. Sci.* 45:19-26.
- Miller, R. M. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. *Ecology* 54:256-272.
- O'Farrell, T. P., R. J. Olson, R. O. Gilbert, and J. D. Hedlund. 1975. A population of Great Basin pocket mice, *Perognathus parvus*, in the shrub-steppe of south-central Washington. *Ecol. Monogr.* 45:1-28.
- Poulton, C. E. 1955. Ecology of the non-forested vegetation in Umatilla and Morrow counties, Oregon. Ph.D. Thesis, Washington State Univ., Pullman. 166 p.
- Rogers, L. E., and R. E. Fitzner. 1980. Characterization of darkling beetles inhabiting radioecology study areas at the Hanford site in southcentral Washington. *Northw. Sci.* 54:202-206.
- Rogers, L. E., and J. D. Hedlund. 1980. A comparison of small mammal populations occupying three distinct shrub-steppe communities in eastern Oregon. *Northw. Sci.* 54:183-186.

Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1976. A general weight vs. length relationship for insects. *Annals of the Entomol. Soc. of Am.* 69:387-389.

Ruffner, J. A. 1978. *Climates of the United States*. Vol. 2. Gale Research Co. Book Tower, Detroit, Mich. 578 p.

Schlatter, R. P., J. L. Yanez, H. Nunez, and F. M. Jaksic. 1980. The diet of the burrowing owl in central Chile and its relation to prey size. *Auk* 97:616-619.

Thomsen, L. 1971. Behavior and ecology of burrowing owls on the Oakland Municipal Airport. *Condor* 73:177-192.

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Aspen Seedlings in Recently Burned Areas of Grand Teton and Yellowstone National Parks

Abstract

Although aspen (*Populus tremuloides*) produces viable seeds most years, seedling establishment has seldom been reported in the western United States. This paper documents the natural establishment of large numbers of aspen seedlings on recently burned areas in Grand Teton and Yellowstone National Parks. Though a few aspen seedlings were widely scattered throughout the 1985 Beaver Creek burn in Grand Teton National Park, the greatest concentrations occurred at the bottom of kettles or other topographic depressions where densities ranged from 925 to 2,708/ha in 1989. In Yellowstone National Park, aspen seedlings were widely distributed over the area burned by the 1988 wildfires on the northern range but the greatest concentrations occurred in riparian zones that had been burned down to bare mineral soil. In those locations aspen seedling densities as high as 11.5×10^6 /ha were recorded and averaged 142,645/ha on permanent plots established in 1989. On permanent plots in the Beaver Creek Burn, the average aspen seedling density increased by 16% from 1989 to 1991 while on permanent plots in Yellowstone Park, aspen seedling densities declined 78% during the same interval. While an abundance of naturally occurring aspen seedlings has not been reported before, evidence suggests that these seedlings may not lead to the growth of mature trees or the development of aspen clones.

Introduction

Throughout the Intermountain West, reproduction of aspen (*Populus tremuloides*) depends almost entirely on the production of adventitious shoots or suckers which arise from lateral roots near the soil surface (Schier *et al.* 1985). Establishment from seed has only occasionally been reported (McDonough 1985). Seedling scarcity is attributed to short-lived seed and demanding seed-bed requirements (Faust 1936, Pauley 1963, Pauley *et al.* 1963, Shier 1981, Jones *et al.* 1985). To grow from seed successfully, aspen seedlings require a combination of bare mineral soil (no competing vegetation), plus high moisture content in surface soils throughout germination and the first growing season. These conditions are frequently met in northern Canada, Alaska, and eastern North America where aspen commonly grow from seed. In the western U.S., however, infrequent rainfalls usually are followed by dry periods which kill any newly germinated seedlings (McDonough 1979, 1985).

Baker (1918, 1925) searched diligently in Utah, southern Idaho, and western Wyoming for 6 years, but failed to find any aspen seedlings even in burned or logged areas. In 25 years of observations, Beetle (1974:9) did not find a single aspen seedling in the Jackson Hole area of western Wyoming. Ellison (1943), though, found one seedling growing near a lake margin on Utah's Aquarius Plateau, while Larson (1944) reported several hundred aspen established from seed on the shoreline of Strawberry Reservoir in central Utah.

Barnes (1966:442) observed "numerous aspen seedlings in northern Idaho, predominantly on recently burned sites" but provided no other information. Every and Wiens (1971:141) found five aspen seedlings at unspecified locations in Utah.

Williams and Johnston (1984) documented aspen seedling establishment on spoil from a phosphate mine in southeastern Idaho. Most seedlings were concentrated around small seeps, though others were found on all parts of the spoil banks. Seedling densities ranged from 20,000 to 100,000/ha. At the end of four growing seasons, 73% of those seedlings were still alive and had attained heights ranging from 16 to 81 cm. Moss (1938:541) and Every and Wiens (1971:146) suggested that periodic aspen seedling establishment may occur in unusually wet years, though they had no evidence to support their contention.

I have found numerous aspen seedlings in northwest Wyoming and southern Montana on recently burned areas within Grand Teton National Park and on Yellowstone National Park's northern range. Unlike other observations which have usually been associated with some type of human disturbance, these seedlings became established under natural conditions following wildfires.

Study Areas

The two study sites reported in this paper lie within the Greater Yellowstone Ecosystem (Clark and Zaunbrecker 1987). Anderson (1958) and Boyce (1989) provide a general description of the climate

and vegetation in Jackson Hole while Dirks (1979), Dirks and Martner (1982), and the National Park Service (1986:12-16) provide more detailed information for Grand Teton National Park. Houston (1982) and Despain (1990) provide a description of the climate, physiography, and vegetation of Yellowstone's northern range.

During late August 1985, the Beaver Creek fire burned approximately 416 ha of mostly coniferous forest in Grand Teton National Park (Sections 10, 11, 14 and 15; T43N, R116W). Fire intensity was sufficient to kill nearly all trees within the burn's perimeter and to exfoliate 8 to 10 cm of stone from granite boulders. The Beaver Creek burn covers the terminal moraine of the glacier that once flowed out of Avalanche Canyon. Much of the area is covered by kettles and kames, and elevation ranged from 2,050 to 2,100 m. Prior to the fire, lodgepole pine (*Pinus contorta*) was the most abundant conifer but stands of Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) were common. Small areas of dry grasslands, riparian zones, and occasional aspen clones were also burned. The Beaver Creek burn is grazed by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) during late spring, summer, and fall as deep snow precludes ungulate use during winter.

During the summer of 1988, approximately 550,000 ha burned in the Greater Yellowstone Ecosystem including a large portion of Yellowstone Park. Approximately 34% of the park's northern range burned, including 8% of dry grasslands, as well as several wet meadows (Singer and Schullery 1989). Elevation ranged from 1,700 m to 2,100 m. Unlike the Beaver Creek burn which is grazed by ungulates during the growing season, Yellowstone's northern range is used by elk and other ungulates primarily during winter, though some summer use does occur (Kay 1990).

Methods

Grand Teton National Park

During the summer of 1988, I found what appeared to be numerous aspen seedlings in the Beaver Creek burn. Several were carefully excavated, photographed, and later verified as aspen seedlings. All had numerous fibrous roots which originated from a central tap root. None were connected to any other aspen via lateral roots as would be the case if they were suckers originating from an aspen clone (Schier 1981). Additional seedlings

were excavated during 1989 and deposited in the Intermountain Herbarium, Utah State University, Logan, Utah. The nearest likely sources of aspen seed ranged from 200 m to 800 m.

I searched the entire Beaver Creek Burn for aspen seedlings in 1989 and placed eight permanent 4 x 30 m belt transects in areas that contained the greatest concentrations of seedlings. The ends of the transects were marked with single steel stakes and a 30 m tape was stretched between those points. A distance of 2 m was measured out to the right and left of the transect centerline. The transect centerline was then divided into 3 m segments. This produced a series of 2 x 3 m counting plots to the right and left of the centerline for a total of 20 counting plots per transect. The number of aspen and lodgepole pine seedlings was recorded on each 2 x 3 m counting plot and summed over the entire length of each transect. The height and any evidence of recent ungulate browsing were recorded for each aspen seedling, and for the tallest lodgepole pine seedling on each of the 20 counting plots per transect.

Percent canopy-coverage of grasses, forbs, shrubs (including aspen seedlings), lodgepole pine seedlings, and bare ground was visually estimated on 0.2 x 0.5 m (0.1 m²) microplots placed adjacent to each belt transect's centerline at 2 m intervals. At each interval, microplots were placed to the right and left of the centerline, except that the transect's beginning and end points were not utilized. Thus, 28 estimates of ground cover were obtained for each 30 m belt transect. All plots were remeasured in August 1991. Aspen seedlings were aged by counting bud scale scars.

The Beaver Creek burn is located approximately 6 km north of park headquarters at Moose, Wyoming where a weather station has been maintained since 1936. That station is about 90 m lower than the burn and may be a little drier (Dirks and Martner 1982). Other weather stations in the valley, such as Jackson or Moran, are even farther removed from the burn and have noticeably different climates (Dirks and Martner 1982). Weather data from 1936 to 1976 were taken from Dirks and Martner (1982) while more recent records were obtained from *Climatological Data: Wyoming* (National Oceanic and Atmospheric Administration 1977-1991).

The mean heights of aspen and lodgepole pine seedlings in 1991 were compared using Student's

t test (Sokal and Rohlf 1981). The other data do not lend themselves to comparative statistical analysis (Hurlbert 1984) or the comparative tests were not germane to this study.

Yellowstone National Park

I searched the northern range for aspen seedlings during August and September, 1989 and then established three 2 x 30 m permanent belt transects in a 100 x 300 m area of Yancy's Hole (Universal Transverse Mercator grid coordinates 4975000N 545300E) where aspen seedlings were abundant. The ends of the transects were marked with single steel stakes and a 30 m tape was stretched between those points. A distance of 1 m was measured out to the right and left of the transect centerline. The transect centerline was then divided into 3 m segments. This provided a series of 1 x 3 m counting plots to the right and left of the centerline for a total of 20 counting plots per transect. The number of aspen seedlings was recorded on each 1 x 3 m counting plot and summed over the entire length of each transect. The height and any evidence of recent or past ungulate browsing was recorded for the tallest aspen seedling on each of the 20 counting plots per transect. Transect centerlines were used to measure canopy-coverage of other species via line intercept (Hanley 1978). In a burned-out 30 x 30 m sedge depression near Range Exclosure 25 (Universal Transverse Mercator grid coordinates 4975800N 545700E), aspen seedlings were so abundant that I recorded their numbers in 1 x 1 m plots. A likely source of aspen seed is situated within 100 m of the Range Exclosure 25 site and within 400 m of the Yancy's Hole site. Several seedlings were excavated and deposited with the Intermountain Herbarium.

Results

New aspen seedlings have only a slight resemblance to the adult form. New seedling leaves are nearly lanceolate instead of the familiar orbicular to broadly ovate shape of normal adult aspen leaves (Figure 1). During the first growing season, seedling leaf petioles are not obviously vertically flattened as they are in the adult form and there is no lateral branching. By the second and third growing seasons, though, seedlings produce lateral branches and normal adult aspen leaves. All plants more than 1-year old identified as aspen seedlings in this study had already produced adult form

aspen leaves. All plants identified as new aspen seedlings in 1989 produced adult form aspen leaves by 1991. These plants are clearly aspen seedlings, not another species of *Populus*.

Grand Teton National Park

Although a few aspen seedlings were widely scattered throughout the Beaver Creek burn, the greatest concentrations occurred at the bottom of kettles or other topographic depressions where densities ranged from 950 to 2,700/ha in 1989 (Table 1). The mean height of all aspen seedlings four years after the fire (1989) was 39 cm; but height is not a true measure of their growth because 85% had already been browsed at least once by ungulates. In 1991, the mean height of the aspen seedlings was 41 cm. This was partly due to the relatively high rate of recent browsing, 43%, and new short-statured seedlings which lowered the average height of the sampled population. Greatest aspen seedling height growth between 1989 and 1991 was observed on belt transects with the lowest incidence of ungulate browsing and where no new seedlings were present (Table 1).

Even though lodgepole pine was abundant throughout the Beaver Creek area prior to the fire, most lodgepole pine seedlings were restricted to the same sites occupied by aspen seedlings. Fire-killed lodgepole pine were present on all transects, and lodgepole pine seedlings averaged 65,379/ha in 1989 but they had decreased to 55,319/ha by 1991 (Table 1). None of the lodgepole pine seedlings showed any evidence of ungulate browsing (Table 1). Mean height of lodgepole pine seedlings was 42 cm in 1989 and they had grown to an average height of 116 cm by 1991 (Table 1).

Vegetation recovery throughout the burn has been slow and probably reflects the intensity of the fire. Four summers after the burn (1989), grasses, forbs, and shrubs had a combined average canopy-coverage of only 28% on the measured transects while 60% of the area was still bare (Table 2). The combined canopy-coverage of grasses, forbs and shrubs had increased to 53% by 1991. Most of that increase was in the forb component (Table 2). Fireweed (*Epilobium angustifolium*), while present, was not particularly abundant. Mountain hollyhock (*Lilium rivularis*) and most regenerating shrubs were heavily grazed by elk and mule deer which probably limited those species' canopy-coverages. Lodgepole pine seedlings averaged



Figure 1. Closeup of unbrowsed 3-month old aspen seedlings collected in 1989 from Yancy's Hole on Yellowstone National Park's northern range. Note the root structure where numerous fibrous roots originate from a central tap root and the absence of any suckering lateral roots. Meter stick for scale.

TABLE 1. Density, height, and ungulate use of aspen and lodgepole pine seedlings on the Beaver Creek burn, Grand Teton National Park.

Belt Transect	Year	Aspen Seedlings			Lodgepole Pine		
		Number per ha	Percent Browsed*	Mean Height (SEM) (cm)	Number per ha	Percent Browsed*	Mean Height (SEM) (cm)
BCB-1	1989	1,500	89	38 (3)	27,332	0	41 (1)
	1991	1,250	80	41 (3)	22,991	0	114 (4)
BCB-2	1989	1,750	95	41 (3)	24,666	0	46 (2)
	1991	1,416	41	50 (4)	21,825	0	117 (4)
BCB-3	1989	1,083	92	41 (5)	6,750	0	42 (3)
	1991	916	91	42 (6)	6,414	0	120 (6)
BCB-4	1989	1,000	67	49 (6)	19,999	0	39 (3)
	1991	3,165	11	21 (3)	17,493	0	111 (5)
BCB-5	1989	952	100	36 (4)	28,810	0	51 (2)
	1991	1,428	58	27 (6)	25,466	0	142 (4)
BCB-6	1989	1,833	86	36 (3)	96,996	0	43 (2)
	1991	1,583	11	61 (4)	89,464	0	136 (3)
BCB-7	1989	1,500	89	29 (3)	114,412	0	42 (2)
	1991	1,916	26	36 (5)	101,876	0	106 (3)
BCB-8	1989	2,708	62	38 (3)	204,069	0	33 (1)
	1991	2,603	24	50 (4)	157,020	0	81 (3)
Mean	1989	1,541	85	39 (2)	65,379	0	42 (2)
	1991	1,785	43	41 (5)**	55,319	0	116 (7)**

*Percentage of total seedlings with evidence of summer ungulate browsing the same year that they were measured.

**t = 8.71, p < .01.

TABLE 2. Percent ground cover on aspen seedling transects in the Beaver Creek burn, Grand Teton National Park.

Aspen Seedling Transect	Year	Percent Bare Ground	Percent Canopy-Coverage			Lodgepole Pine
			Grass	Forbs	Shrubs	
BCB-1	1989	63	11	20	2	4
	1991	29	6	38	2	25
BCB-2	1989	57	22	15	1	5
	1991	17	26	30	3	24
BCB-3	1989	58	13	23	4	2
	1991	20	40	24	4	12
BCB-4	1989	44	28	16	9	3
	1991	12	38	24	9	17
BCB-5	1989	78	2	10	0	10
	1991	28	6	26	2	38
BCB-6	1989	64	4	10	1	22
	1991	7	1	42	1	49
BCB-7	1989	75	1	9	0	16
	1991	6	4	49	1	40
BCB-8	1989	41	23	5	3	28
	1991	1	18	28	2	51
Mean	1989	60	13	13	2	11
	1991	15	17	33	3	32

11% canopy-coverage in 1989 and 32% in 1991. By 1991, the proportion of exposed mineral soil/rock had decreased to 15%.

Grand Teton Park and much of the Intermountain West experienced a drought from 1986 through 1988. Precipitation at Moose was only 63 to 71% of the 50-year average of 617 mm. June, July, and August were particularly dry with precipitation only 16% to 70% of the 50-year means, except for July 1987 when precipitation was 2.5 times above average. Precipitation during June, July, and August 1989 was above average and for the year was nearly normal. But in 1990, precipitation again was only 72% of average. During the 1990 and 1991 growing seasons, precipitation was below average in four of the six months. The amount and timing of rainfall certainly were not within the range commonly thought necessary for aspen seed germination and seedling survival, except perhaps for July 1987 (McDonough 1979, 1985). Daily temperatures during the June-August growing seasons were usually within the range reported for aspen seed germination and seedling growth (McDonough 1979) except that frosts occurred at least 50 times from 1986 to 1991.

Despite the fact that elk and mule deer had browsed a high proportion of the terminal leaders on aspen seedlings (Table 1), I was able to age a random sample of 222 aspen seedlings in 1989 by counting the bud scars on lateral branches and the lower, unbrowsed main stems. Some aspen seedlings became established and survived each year after the fire; 23% began growth in 1986, 60% in 1987, 14% in 1988, and 4% in 1989. The greatest proportion of seedlings began growth in 1987 when July temperatures and precipitation were most favorable. New aspen seedlings were also observed on three of the permanent belt transects in 1991 (BCB-4, 5, and 7; Table 1).

In all years, kettle bottoms and other topographic depressions apparently held the additional soil moisture needed for aspen seedling establishment. Several kettles in the burn contained standing water year-long while others held water during spring.

Yellowstone National Park

The 1988 fires occurred during an extended drought and under extreme burning conditions (Davis and Mutch 1989; Romme and Despain 1989a, 1989b; Schullery 1989a, 1989b). This

permitted the fires to burn normally wet riparian zones including seeps and lake margins (Knight and Wallace 1989). Many of those areas had thick sedge (*Carex* spp.) mats and accumulations of organic matter that "were burned down to mineral soil, killing rhizomes and root systems" (Knight and Wallace 1989:704). At the time of aspen seed release during spring 1989, these areas of bare mineral soil and ash held abundant moisture (Figure 2).

Aspen on the northern range produced a prolific seed crop during spring 1989 and temperatures and precipitation were also favorable for aspen seed germination and seedling growth. This combination of factors produced an abundance of aspen seedlings during the summer of 1989. On belt transects in a burned-out sedge meadow in Yancy's Hole, aspen seedlings averaged 142,695/ha (Table 3, Figures 2 and 3). The fire had killed the sedges and the newly established competing vegetation had an average canopy-coverage of only 12% (Table 3). In another burned-out sedge depression near Range Enclosure 25, the average density of aspen seedlings on five 1 m² plots was 1,152/m² (sd = 410) or over 11.5 x 10⁶/ha. By 1991, the mean density of aspen seedlings on the Yancy's Hole belt transects had declined to 31,654/ha while the canopy-coverage of other plants increased to 69% (Table 3). From 1989 to 1991, average height of the aspen seedlings declined from 58 cm to 47 cm. By 1991, all aspen seedlings showed signs of repeated ungulate browsing (Table 3) which probably accounts for the height loss, as new aspen seedlings were not observed in 1991. None of the aspen seedlings showed any evidence of summer ungulate browsing in 1989 or 1991. The incidence of browsing recorded in 1991 apparently occurred during the winters of 1989-90 and 1990-91.

During the summer of 1989, I also observed widely scattered aspen seedlings in burned coniferous forests and even within established aspen stands killed by fire. The tallest observed seedling measured 78 cm and had 24 leaves. Areas with the most abundant seedlings usually had ash deposits 1-5 cm thick on top of mineral soil, suggesting that the ash may have promoted aspen seed germination and survival. This factor apparently has not been previously investigated in studies of aspen seed germination and survival (McDonough 1979, 1985).



Figure 2. Burned-out sedge meadow in Yancy's Hole near Tower Junction on Yellowstone National Park's northern range in 1989. Prior to the 1988 fires, this area was a continuous sedge meadow with no openings. The burned-out areas were covered with standing water until mid-June 1989. The aspen seedling belt transects are located in the lower-left center.

TABLE 3. Aspen seedling parameters and vegetation ground cover in Yancy's Hole, Yellowstone National Park.

Belt Transect	Year	Number of Aspen Seedlings per ha	Mean Height (SEM) (cm)*	Percent Browsed**	Percent Canopy-Coverage of Other Vegetation
AS-1	1989	177,202	62 (3)	—	12
	1991	32,154	50 (4)	100	65
AS-2	1989	141,362	60 (4)	—	7
	1991	46,148	57 (5)	100	68
AS-3	1989	109,522	53 (7)	—	18
	1991	16,660	34 (3)	100	75
Mean	1989	142,695	58 (3)	—	12
	1991	31,654	47 (7)	100	69

*Mean height of 20 tallest seedlings per belt transect; see text.

**Percent of seedlings that showed evidence of past browsing. This site is grazed during winter and none of the aspen seedlings showed any evidence of summer browsing when they were measured in 1989 or 1991; see text.



Figure 3. Newly grown aspen seedlings on a permanent belt transect in Yancy's Hole, Yellowstone National Park. Nearly all the plants in this 1989 photograph are aspen seedlings. Aspen seedling density on this transect was 141,362/ha and other species had a canopy-coverage of 7%.

Discussion

Most seedlings and certainly their greatest concentrations were associated with seeps, springs, topographic depressions, or other microsites with abundant soil moisture, conditions that have been established experimentally for aspen seed germination and seedling development (McDonough 1979, 1985). Zasada *et al.* (1983) reported that in interior Alaska aspen seedling establishment and survival was positively correlated with burning intensity. Aspen seedling survival occurred almost exclusively on severely burned surfaces. All of the aspen seedlings observed in Grand Teton and Yellowstone National Parks were associated with bare mineral soil, ash, and an absence of competing vegetation following wildfires. So it appears that high intensity fires may be required for aspen seedling establishment in the West.

Fire has often been used to regenerate established aspen stands because fire-killed trees produce abundant root suckers (Schier 1981, Schier *et al.* 1985). In the upper Gros Ventre drainage of Jackson Hole, aspen sucker densities ranged from 24,000 to 36,000/ha 2 years after the 200 ha Breakneck Ridge aspen burn (Bartos and Mueggler 1981). On other burns in Jackson Hole, aspen sucker densities ranged from 10,000 to 150,000/ha (Bartos *et al.* 1991). One year after the fires on Yellowstone's northern range, burned aspen stands produced sucker densities of 1,000 to 200,000/ha (Kay unpub. data). So, the densities of aspen seedlings on the Beaver Creek burn are much lower than sucker densities which normally occur after established aspen stands are burned. On the other hand, aspen seedling densities on Yellowstone's burned-out sedge meadows were up to 50 times greater than highest aspen sucker densities recorded after the 1988 fires.

Despite an abundance of naturally occurring aspen seedlings in these areas, several lines of evidence suggest that they likely will not lead to the development of mature trees or aspen clones. First, many of the burned-out sedge meadows and other topographic depressions in Yellowstone that contain the highest densities of aspen seedlings are subject to spring flooding. During years of abundant precipitation, these areas may hold water for most of the summer (Brichta 1987, Chadde *et al.* 1988). Since aspen do not tolerate standing water, these seedlings will die if they are flooded for any length of time. This probably explains the

reduction of aspen seedlings that occurred on the belt transects in Yancy's Hole, though ungulate browsing and self-thinning may also have been factors.

Second, both study areas have large populations of elk and other ungulates for which aspen is a preferred food. Large numbers of elk now summer in Grand Teton National Park (Boyce 1989) and most of the aspen seedlings in the Beaver Creek burn have been browsed at least once. Elk appear capable of preventing aspen seedling height growth and their development into trees. Elk have prevented height growth of aspen suckers which sprouted in fire-killed aspen stands throughout Jackson Hole (Bartos and Mueggler 1981, Kay 1990).

In Yellowstone, 15,000 to 25,000 elk winter on the northern range (Houston 1982, Lemke and Singer 1989, Singer and Schullery 1989). Unprotected aspen in the park have not been able to regenerate vegetatively for the last 80 or more years because of repeated browsing (Kay 1990). With the level of ungulate use that exists in Yellowstone, it is questionable whether any of the aspen seedlings will grow into mature trees, let alone establish new clones.

Third, in Grand Teton's Beaver Creek burn, the areas with the greatest concentrations of aspen seedlings also have much higher densities of lodgepole pine seedlings (Table 1). Between 1989 and 1991, lodgepole pine seedlings increased in height by an average of 176% while aspen seedlings grew only 5%. By 1991, lodgepole pine seedlings were also significantly taller than aspen seedlings and, unlike aspen seedlings, had not been browsed by ungulates (Table 1). Lodgepole will probably outgrow the aspen seedlings and dominate those sites.

Fourth, during an extensive survey of established aspen stands in and adjacent to Grand Teton and Yellowstone Parks, I observed very few aspen clones growing on sites similar to those occupied by the aspen seedlings described herein (Kay 1985, 1990, and unpub. data). For example, only twice were fire-killed aspen observed in or adjacent to kettles or other topographic depressions in the Beaver Creek burn, and those were single trees. Most of the established stands in this burn are on south-to-east-facing hillsides.

On Yellowstone's northern range, few aspen stands are established along lake margins, in sedge meadows, or topographic depression where aspen

seedlings are now most abundant (Kay 1985, 1990; Chadde *et al.* 1988). A few aspen grow near seeps or springs, but that is relatively uncommon. Most established aspen stands are not associated with high water tables, which is not surprising since, as noted previously, aspen seldom survive on saturated soils. This creates a paradox since the sites most favorable to seed germination and seedling growth may not be favorable for the establishment of mature aspen trees or clones. In interior Alaska, Krasny *et al.* (1988) reported that aspen seedlings readily established on river bars but that they seldom grew into mature trees due to repeated spring flooding.

Most aspen clones in the West are larger than those found in other areas of North America (Kemperman and Barnes 1976). Randomly selected clones that I measured on Yellowstone's northern range ($n = 268$) averaged 0.5 ha, while the largest covered 6.8 ha (Kay 1990). A single aspen clone in southern Utah occupied 43.3 ha, though larger clones probably exist (Kemperman and Barnes 1976). Due to the large size of these clones and the heretofore lack of observed sexual reproduction, it has been postulated that western aspen clones may be 8 to 10,000 or more years old (Jones and DeByle 1985:35). The abundance of large numbers of aspen seedlings in Grand Teton and Yellowstone National Park, though, suggests that catastrophic fires may be important in the establishment of aspen from seed and that establish-

ment of aspen clones in the West may not be as rare as commonly believed.

I would caution, however, that seedling occurrence, in and of itself, may not be sufficient to establish aspen clones under present conditions. Since Yellowstone Park was established in 1872, repeat photographs ($n = 81$) show that the area occupied by aspen has declined by approximately 95% and that at least one-third of the clones have totally disappeared due to repeated browsing by elk and other native ungulates, not climatic factors (Kay 1990). Only inside ungulate-proof enclosures have established aspen clones expanded in size (Kay 1990), as would be required if aspen clones established from seed.

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Literature Cited

- Anderson, C. C. 1958. The elk of Jackson Hole, Wyoming. Game and Fish Comm. Bull. 10. 184 p.
- Baker, F. S. 1918. Aspen reproduction in relation to management. J. For. 16:389-398.
- Baker, F. S. 1925. Aspen in the central Rocky Mountain region. U.S. Dept. Agr. Bull. 1291. 47 p.
- Bartos, D. L., W. F. Mueggler, and R. B. Campbell, Jr. 1991. Regeneration of aspen by suckering on burned sites in western Wyoming. U.S. For. Ser. Res. Paper INT-448. 10 p.
- Bartos, D. L. and W. F. Mueggler. 1981. Early succession in aspen communities following fires in western Wyoming. J. Range Manage. 34:315-318.
- Barnes, B. V. 1966. The clonal growth habit of American aspens. Ecology 47:439-447.
- Beetle, A. A. 1974. Range survey in Teton County, Wyoming. Part IV. Quaking aspen. Univ. of Wyoming, Agr. Exp. Station. SM27. 28 p.
- Boyce, M. S. 1989. The Jackson elk herd: Intensive wildlife management in North America. Cambridge University Press, Cambridge. 306 p.
- Brichta, P. H. 1987. Environmental relationships among wetland community types on the northern range, Yellowstone National Park. M.S. Thesis, Univ. of Montana, Missoula. 67 p.
- Chadde, S. W., P. L. Hansen, and R. D. Pfister. 1988. Wetland plant communities on the northern range of Yellowstone National Park. School of Forestry, Univ. of Montana, Missoula. Final contract report to National Park Service. 81 p.
- Clark, T. W. and D. Zaunbrecher. 1987. The greater Yellowstone ecosystem: The ecosystem concept in natural resource policy and management. Renewable Resources J. 5(3):8-16.
- Davis, K. M. and R. W. Mutch. 1989. The fires of the greater Yellowstone area: The saga of a long hot summer. Western Wildlands 15(2):2-9.
- Despain, D. 1990. Yellowstone vegetation. Roberts Rinehart Publishers, Boulder, CO. 239 p.
- Dirks, R. A. 1979. Climatological studies in Yellowstone and Grand Teton National Parks. National Park Service Trans. and Proc. Series 5. Vol. 1:49-56.
- Dirks, R. A. and B. E. Martner. 1982. The climate of Yellowstone and Grand Teton National Parks. National Park Service Occ. Paper 6. 26 p.

- Ellison, L. 1943. A natural seedling of western aspen. *J. For.* 41:767-768.
- Every, A. D. and D. Wiens. 1971. Triploidy in Utah aspen. *Madrono* 21:138-147.
- Faust, M. E. 1936. Germination of *Populus grandidentata* and *P. tremuloides* with particular reference to oxygen consumption. *Bot. Gaz.* 97:808-821.
- Hanley, T. A. 1978. A comparison of the line-interception and quadrat estimation methods of determining shrub canopy coverage. *J. Range Manage.* 31:60-62.
- Houston, D. B. 1982. The northern Yellowstone elk: Ecology and management. MacMillan Pub., NY. 474 p.
- Hurlbert, S. H. 1984. Pseudo-replication and design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- Jones, J. R., M. R. Kaufmann, and E. A. Richardson. 1985. Effects of water and temperature. In N. V. DeByle and R. P. Winokur (eds.) *Aspen: Ecology and management in the western United States*. U.S. For. Serv. Gen. Tech. Rep. RM-119. Pp. 71-76.
- Jones, J. R., and N. V. DeByle. 1985. Genetics and variation. In N. V. DeByle and R. P. Winokur (eds.) *Aspen: Ecology and management in the western United States*. U.S. For. Serv. Gen. Tech. Rep. RM-119. Pp. 35-39.
- Kay, C. E. 1985. Aspen reproduction in the Yellowstone Park-Jackson Hole area and its relationship to the natural regulation of ungulates. In G. W. Workman (ed.) *Western elk management: A symposium*. Utah State Univ., Logan. Pp. 131-160.
- _____. 1990. Yellowstone's northern elk herd: A critical evaluation of the "natural regulation" paradigm. Ph.D. Diss., Utah State Univ., Logan. 490 p.
- Kemperman, J. A. and B. V. Barnes. 1976. Clone size in American aspens. *Can. J. Bot.* 54:2603-2607.
- Knight, D. H. and L. L. Wallace. 1989. The Yellowstone fires: Issues in landscape ecology. *Bioscience* 39:700-706.
- Krasny, M. E., K. A. Vogt, and J. C. Zasada. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Holarct. Ecol.* 11:210-219.
- Larson, G. C. 1944. More on seedlings of western aspen. *J. For.* 42:452.
- Lemke, T. and F. J. Singer. 1989. Northern Yellowstone elk: The big herd. *Bugle* 6(4):113-121.
- McDonough, W. T. 1979. Quaking aspen seed germination and early seedling growth. U.S. For. Serv. Res. Paper INT-234. 13 p.
- _____. 1985. Sexual reproduction, seeds and seedlings. 1989. In N. V. DeByle and R. P. Winokur (eds.) *Aspen: Ecology and management in the western United States*. U.S. For. Serv. Gen. Tech. Rep. RM-119. Pp. 25-28.
- Moss, E. H. 1938. Longevity of seed and establishment of seedlings in species of *Populus*. *Bot. Gaz.* 99:529-542.
- National Oceanic and Atmospheric Administration. 1977-1991. Climatological data: Wyoming. Vol. 86-100.
- National Park Service. 1986. Natural resources management plan and environmental assessment: Grand Teton National Park. Rocky Mountain Regional Office, Denver, CO. May 27. 473 p.
- Pauley, S. S. 1963. Performance of some aspen seed sources and hybrids in eastern Massachusetts. In *World Consultation on Forest Genetics and Tree Improvement*, Stockholm, 1963. Food and Agricultural Organization of the United Nations, Rome, Italy. FAO/Forgen 63-2b/2.
- Pauley, S. S., A. G. Johnson, and F. S. Santamour, Jr. 1963. Results of aspen screening tests: I. Seed sources of quaking aspen (*P. tremuloides* Michaux). School of Forestry, Univ. of Minnesota, Minnesota Forestry Notes 136:1-2.
- Romme, W. H., and D. G. Despain. 1989a. Historical perspective on the Yellowstone fires of 1988. *Bioscience* 39:695-699.
- Romme, W. H., and D. G. Despain. 1989b. The Yellowstone fires. *Sci. Amer.* 261(5):37-46.
- Schier, G. A. 1981. Aspen regeneration. In N. V. DeByle (ed.) *Symposium proceedings—situation management of two intermountain species: Aspen and coyotes*, Vol. I—*aspen*. Utah State Univ., Logan. Pp. 15-21.
- Schier, G. A., W. D. Shepperd, and J. R. Jones. 1985. Regeneration. In DeByle, N. V. and R. P. Winokur (eds.) *Aspen: Ecology and management in the western United States*. U.S. For. Serv. Gen. Tech. Rep. RM-119. Pp. 197-208.
- Schullery, P. 1989a. Yellowstone fires: A preliminary report. *NW Sci.* 63:44-54.
- _____. 1989b. The fires and fire policy. *Bioscience* 39:686-694.
- Singer, F. J. and P. Schullery. 1989. Yellowstone wildlife: Populations in process. *Western Wildlands* 15(2):18-22.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry: The principles and practice of statistics in biological research*. 2nd ed. W. H. Freeman and Co., San Francisco. 859 p.
- Williams, B. D. and R. S. Johnston. 1984. Natural establishment of aspen from seed on a phosphate mine dump. *J. Range Manage.* 37:521-522.
- Zasada, J. C., R. A. Norum, R. M. Van Veldhuizen, and C. E. Teutsch. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feathermoss stands in Alaska. *Can. J. For. Res.* 13: 903-913.

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Distribution and Movements of White Sturgeon in Three Lower Columbia River Reservoirs

Abstract

We determined the distribution and movement of white sturgeon (*Acipenser transmontanus*) in Bonneville, The Dalles, and John Day reservoirs on the Columbia River from April through August, 1987-1991. The study also evaluated effects of hydroelectric dams on white sturgeon populations. Differences in catch per setline-day indicated that white sturgeon densities were greatest in Bonneville Reservoir and least in John Day Reservoir. White sturgeon concentrated in tailraces of dams and density generally declined downstream through each reservoir. Distribution within each reservoir varied with sampling month and were related, in part, to temperature. Most fish were caught at depths from 10 to 30 m. Tagged fish were often recaptured in locations other than those where originally marked. Some fish were recaptured as far as 152 km from where released. Individual fish frequently traveled the length of a reservoir, but were seldom recaptured in another reservoir. Dams restrict white sturgeon movements, may limit populations in some reservoirs, and concentrate fish immediately downstream, potentially increasing their vulnerability to exploitation. To optimize these fisheries, resource managers must recognize differences among reservoirs and employ regulatory schemes specific to each.

Introduction

The white sturgeon (*Acipenser transmontanus*) is a unique and ancient species endemic to large, cool rivers along the Pacific coast of North America. White sturgeon are among the largest freshwater fish in North America, exceeding 6 m and 800 kg (Scott and Crossman 1973). In the Columbia River basin, white sturgeon historically ranged from the ocean as far as 1300 km upstream into Idaho, Montana, and Canada. Individual fish were thought to have moved freely throughout the area (Scott and Crossman 1973). Sturgeon regularly undertook long-distance movements, apparently to take advantage of seasonal changes in food and habitat in this dynamic river environment (Bajkov 1951).

Dams, constructed on the mainstem Columbia since 1933, limit the distribution and constrain movements of sturgeon which, unlike salmon, do not normally use fish ladders. Cochnauer *et al.* (1985) suggested that white sturgeon populations in some landlocked portions of the river were isolated with respect to reproduction. Productivity appeared to vary among populations as some supported fertile fisheries while others could sustain no exploitation (Cochnauer *et al.* 1985). Also, dams may have led to genetic divergence of impounded populations due to reproductive isolation (Brown *et al.* 1992).

Understanding the distribution and movement of white sturgeon in landlocked populations may

help determine why some populations thrive while others appear to be in danger of extirpation. Size-specific seasonal movements have been observed for landlocked white sturgeon in the unimpounded Hanford Reach of the mid-Columbia River (Haynes *et al.* 1978, Haynes and Gray 1981), but no information exists for impounded populations. This paper investigates white sturgeon distribution and movement within and among the lower Columbia River reservoirs.

Study Area

The study area included the three lowest mainstem reservoirs of the Columbia River: Bonneville (Lake Bonneville), The Dalles (Lake Celilo), and John Day (Lake Umatilla). Bonneville Reservoir (74 km; 8400 ha) is relatively shallow (average depth 6.7 m) with mostly sand substrate supporting large beds of rooted aquatic macrophytes during the summer. The Dalles Reservoir is the smallest (38 km; 4500 ha; average depth 7.5 m), and the most riverine, with cobble, gravel, and sand substrates distributed throughout most of its length. John Day Reservoir is the largest (123 km; 21,000 ha; average depth 8.0 m) and the most diverse. The reservoir grades from a riverine upper section with gravel and cobble substrates to a shallow transition section with sand substrate, and finally to a lentic lower section with steep cliff and boulder banks. Average daily river discharge through the study area ranges seasonally from 3000 to over 12,000 m³/s.

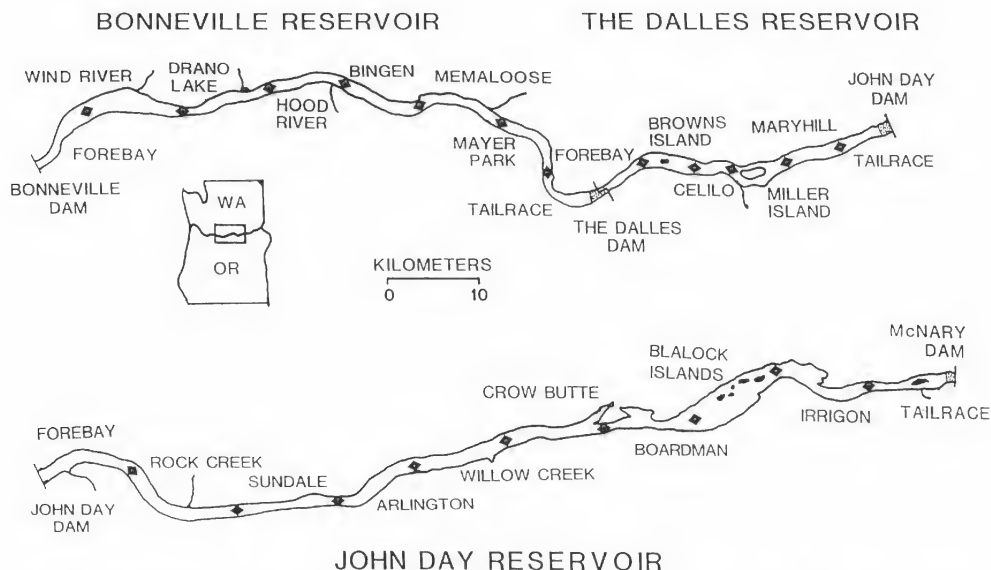


Figure 1. Columbia River from Bonneville to McNary Dams. Sampling area boundaries are indicated by ◆'s. Boat-restricted zones in dam tailraces are shaded.

Methods

To estimate population statistics, we collected white sturgeon during 1988-1989, and 1991 in Bonneville Reservoir; 1987-1989 and 1991 in The Dalles Reservoir; and 1990-1991 in John Day Reservoir. Stratified sampling was conducted from April through September in 1987 and 1990, May through August in 1988, April through August in 1989, and July through August in 1991. We divided Bonneville Reservoir into eight 10-km segments, The Dalles Reservoir into six 7-km segments, and John Day Reservoir into ten 12.5-km segments (Figure 1). We also sampled the boat-restricted zones (BRZ's) which are less than 0.3 km long, and immediately downstream from The Dalles, John Day, and McNary dams. The BRZ's are unlike the remainder of the reservoir because the adjacent dam concentrates and injures potential prey fishes and creates eddies and still water nearby for predators. Because BRZ's are unique habitats, their results are reported separately.

Sampling was distributed equally among segments and river kilometer sampling sites in each reservoir to obtain representative population samples. Each segment was normally sampled every 4 weeks in Bonneville Reservoir, every 3 weeks

in The Dalles Reservoir, and every 5 weeks in John Day Reservoir. From April through June in 1991, we concentrated our sampling locations where we caught most sturgeon in previous years.

White sturgeon were collected using setlines which provide the greatest catch rate and are less size-selective than other types of gear (Elliott and Beamesderfer 1990). Each line had 40 hooks (sizes 12/0, 14/0, and 16/0) baited with pieces of Pacific lamprey (*Lampetra tridentata*). We fished lines for an average 24.8 hr per set. Sets were concentrated in main-channel habitats outside navigational lanes at depths from 3 to 51 m.

We measured sturgeon fork length (FL) to the nearest cm and examined each fish for tags. Untagged sturgeon longer than 64 cm were spaghetti tagged at the anterior base of the dorsal fin. Sturgeon longer than 84 cm were tagged with a second spaghetti or Petersen disc dangler tag at the base of the posterior end of the dorsal fin (Smith 1978). A total of 7351 fish were tagged with individually numbered spaghetti and disc tags. The Washington Department of Fisheries (WDF) also provided tag recoveries from the recreational and commercial fisheries in the three reservoirs and in the free-flowing river between Bonneville Dam and the ocean.

We examined white sturgeon distribution by comparing setline catch rate among areas. Statistical differences ($p < 0.05$) in catch rates were evaluated on transformed catch per set data [$\ln(\text{catch} + 1)$] with programs of the Statistical Analysis System (SAS 1988a, SAS 1988b). To examine seasonal changes in distribution within each reservoir, we used an index (I) where:

$$I = \frac{S - L}{T}$$

and S is river km where fish were captured, L is river km of the lower reservoir boundary, and T is reservoir length in km. The values were averaged for all fish captured during a sampling cycle. A high river kilometer index indicates upstream distribution; a low index indicates downstream distribution. We assumed that seasonal changes in average catch rates implied changes in movement rates. The relationship between catch and water temperature was evaluated using linear regression.

We compared numbers of fish released and recaptured at each site to estimate the extent of movement within each reservoir and to determine whether individuals moved among reservoirs. Recaptures included all fish caught with setlines, and sport and commercial fisheries, where the kilometer of capture could be determined.

Results

Distribution

White sturgeon were not evenly distributed among study reservoirs. Average setline catch per day in Bonneville Reservoir 4.10 fish/set in 942 sets) was 1.5 times greater than in The Dalles Reservoir (2.70 fish/set in 978 sets), and 7.5 times greater than in John Day Reservoir (0.55 fish/set in 1194 sets). Catch rate differences among reservoirs were statistically significant (Table 1).

Densities (catch per day, 1987-1990) of white sturgeon were greater in the BRZ downstream of each dam than in the rest of the reservoir by 3 times in Bonneville Reservoir, 6 times in The Dalles Reservoir, and over 20 times in John Day Reservoir. Densities outside BRZ's generally decreased with distance from the dam (Figure 2). Catch rates outside BRZ's approached those near dams only at the mouth of the Klickitat River (Memaloose segment) in Bonneville Reservoir. Catch rate differences among segments were significant in all three reservoirs (Table 1).

TABLE 1. Statistical comparisons of log-transformed catch [$\ln(\text{catch} + 1)$] of white sturgeon per setline day in Bonneville, The Dalles, and John Day reservoirs, 1987-1990. The Analyses of Variance (ANOVA) are one-way comparisons except Catch vs. depth*size which evaluates interaction in a two-way ANOVA.

Comparison	Reservoir	df*	df ₂ *	F*	p*
Catch vs. reservoir	—	2	3,111	774.60	0.0001
Catch vs. area	Bonneville	8	933	12.00	0.0001
	The Dalles	6	971	43.62	0.0001
	John Day	10	1,183	75.06	0.0001
Catch vs. month	Bonneville	4	922	39.48	0.0001
	The Dalles	4	930	12.40	0.0001
	John Day	5	1,144	6.78	0.0001
Catch vs. depth	Bonneville	6	916	2.89	0.0086
	The Dalles	6	927	2.37	0.0282
	John Day	6	1,142	1.49	0.1783
Catch vs. depth*size	Bonneville	12	2,748	1.38	0.1676
	The Dalles	12	2,781	2.08	0.0153
	John Day	12	3,426	1.48	0.1237

*Degrees of freedom (df), test statistic (F), and observed probability level (p) in ANOVA.

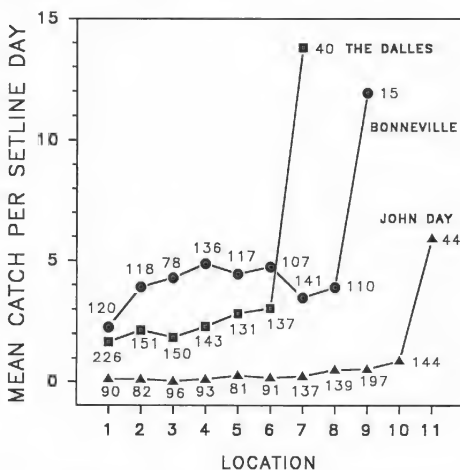


Figure 2. Mean catch per setline day of white sturgeon in Bonneville, The Dalles, and John Day reservoirs, 1987-1990. Number of sets indicated for each reservoir segment. Locations are: Bonneville Reservoir; 1=Forebay, 2=Wind River, 3=Drano Lake, 4=Hood River, 5=Bingen, 6=Memaloose, 7=Mayer Park, 8=Tailrace, 9=The Dalles Dam boat-restricted zone (BRZ). The Dalles Reservoir; 1=Forebay, 2=Browns Island, 3=Celilo, 4=Miller Island, 5=Maryhill, 6=Tailrace, 7=John Day Dam BRZ. John Day Reservoir; 1=Forebay, 2=Rock Creek, 3=Sundale, 4=Arlington, 5=Willow Creek, 6=Crow Butte, 7=Boardman, 8=Blalock Islands, 9=Irrigon, 10=Tailrace, 11=McNary Dam BRZ.

Seasonal changes in distribution were noted in The Dalles and John Day reservoirs. Relative numbers of white sturgeon collected in midreservoir increased from April through June and declined by August and September, implying downstream and then upstream redistribution of fish (Figure 3). Differences in catch proportions in lower, middle, and upper thirds of each reservoir were related to month (Bonneville: $X^2 = 186.75$; $df = 8$; $p < 0.001$; The Dalles: $X^2 = 1,197.19$; $df = 10$; $p < 0.001$; John Day: $X^2 = 334.78$; $df = 10$; $p < 0.001$).

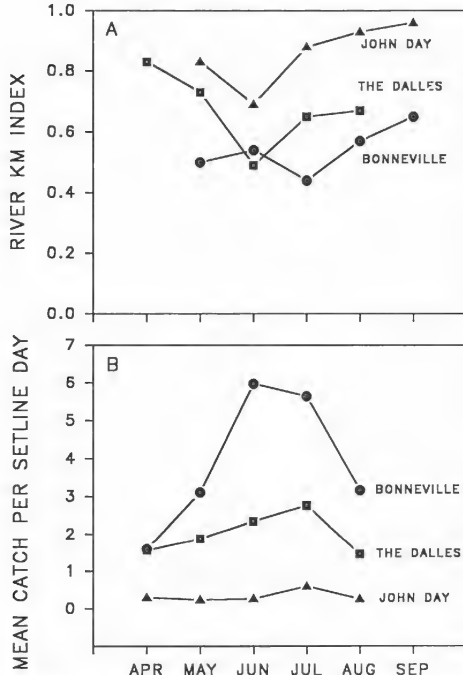


Figure 3. Index of white sturgeon distribution (A) and mean catch per setline day (B) in Bonneville, The Dalles, and John Day reservoirs, 1987-1990. The index is the mean kilometer of capture of all white sturgeon caught during a month. The index is standardized for reservoir size by subtracting the lower reservoir bound and dividing by reservoir size. Sturgeon collected in tailrace boat-restricted zones are excluded.

Catch rates in all three reservoirs peaked in June or July. Monthly differences in catch rates were significant (Table 1). Mean monthly catch rate generally increased with increasing temperature up to about 18°C and declined at greater temperatures (Figure 4). Linear regressions show that about

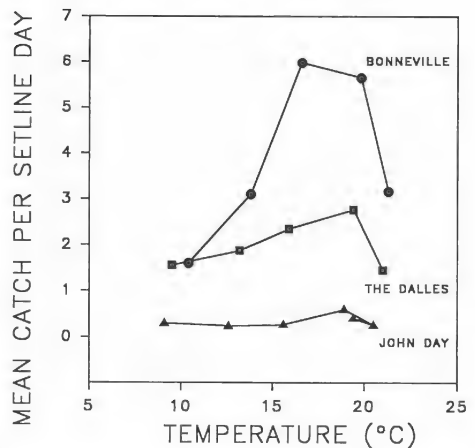


Figure 4. Mean catch of white sturgeon per setline day versus mean monthly temperature for Bonneville, The Dalles, and John Day reservoirs, 1987-1990. Sturgeon collected in the tailrace boat-restricted zones are excluded.

10-30% of the catch rate variation is related to water temperature (Bonneville: $df = 3$, $r^2 = 0.32$, $p = 0.32$; The Dalles: $df = 3$, $r^2 = 0.09$, $p = 0.62$; John Day: $df = 4$, $r^2 = 0.17$, $p = 0.41$).

Catch rates at different depths were significantly different, except in John Day Reservoir where sampling success was poor (Table 1). Few white sturgeon were captured at depths less than 10 m (Figure 5). No meaningful size-depth relationship was evident (Figure 6), although a statistically significant size-depth interaction was noted for The Dalles Reservoir (Table 1).

Movements

Movements up to 152 km were observed among tagged sturgeon. Of 635 tagged individuals, 59% moved at least 1 km and many moved 10-30 km (Figure 7). Average distance traveled between release and recapture was 8.1 km. Of sturgeon that moved between tagging and recapture, 49.9% moved upriver and 50.1% moved downriver. Differences in fish size did not appear to affect distance or direction of fish travel.

Most movement was restricted to the collection reservoir and the extent of movement was related to reservoir length (Figure 7). Only 4% of 635 recaptured white sturgeon moved past a dam in the study area (Table 2). Of these, 26 moved downstream, and 1 moved upstream.

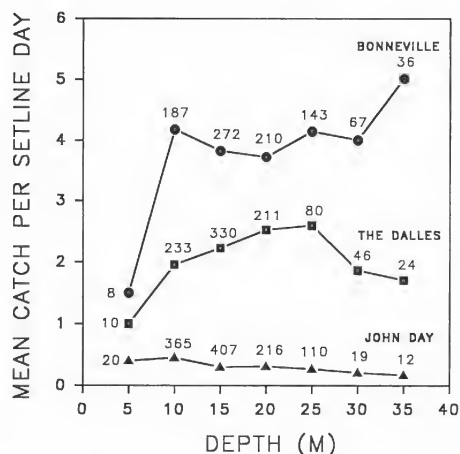


Figure 5. Mean catch of white sturgeon per setline day by 5-m depth intervals for Bonneville, The Dalles, and John Day reservoirs, 1987-1990. Number of sets is indicated for each depth interval. Sturgeon collected in the tailrace boat-restricted zones are excluded.

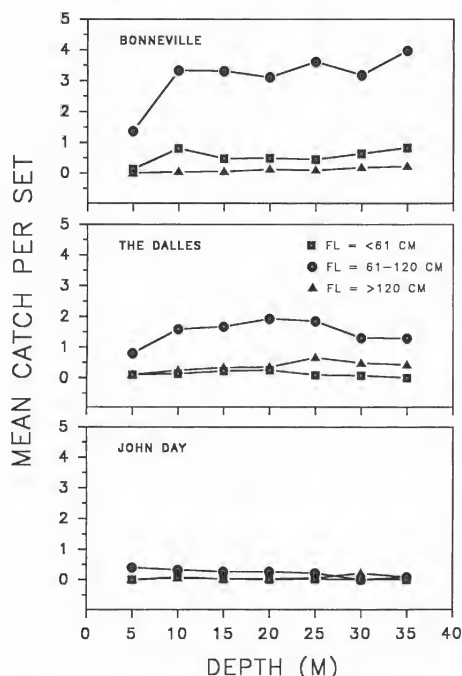


Figure 6. Mean catch of three size-classes of white sturgeon per setline day by 5-m depth intervals for Bonneville, The Dalles, and John Day reservoirs, 1987-1990. Number of sets is indicated for each depth interval. Samples collected in the tailrace boat-restricted zones are excluded.

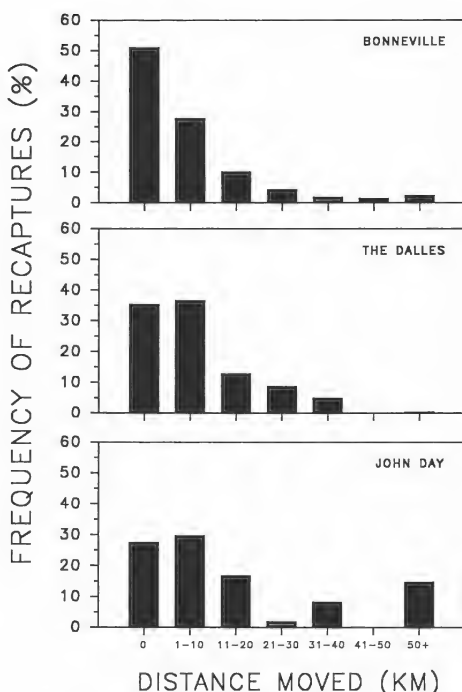


Figure 7. Frequency of white sturgeon recaptures by distance traveled between release and recapture in Bonneville, The Dalles, and John Day reservoirs, 1987-1991.

Discussion

The large differences observed in white sturgeon densities in the three study reservoirs may reflect differences in reproductive success, exploitation rate, and habitat availability. Regular year-class failures in John Day Reservoir, and to a lesser degree in The Dalles Reservoir (Anders and Beckman 1992) may have reduced white sturgeon numbers in these reservoirs. Recently, commercial fisheries have increased their exploitation of white sturgeon. John Day and The Dalles reservoirs were fished more than Bonneville Reservoir from 1980 to 1990 (personal communication, S. King, Oregon Department of Fish and Wildlife, Clackamas, Oregon). Finally, each reservoir has different physical conditions that may furnish critical resources in varying amounts. Although past fishery management has treated the three reservoirs as a homogeneous unit, our data imply that unique size or catch limits may be necessary to optimize the fishery in each.

TABLE 2. Number of tagged white sturgeon released in Bonneville, The Dalles, or John Day reservoirs and recaptured in another reservoir or outside the study area, 1987-1991.

Release location	Recapture location	Recapture year					Total
		1987	1988	1989	1990	1991	
Bonneville	Below Bonneville	—	—	3	4	1	8
The Dalles	Bonneville	—	—	3	3	10	16
John Day	Bonneville	—	—	—	—	1	1
John Day	The Dalles	—	—	—	—	1	1
The Dalles	John Day	1	—	—	—	—	1

The small, unique areas in the tailraces immediately downstream of each dam (BRZ's) yielded high catch rates throughout the study. Beamesderfer and Rieman (1991) reported similar concentrations near dams for another resident predator, the northern squawfish (*Ptychocheilus oregonensis*). Increased food availability may explain these concentrations as these predators eat migrating salmonids (*Oncorhynchus* spp.), shad (*Alosa sapidissima*), and Pacific lamprey that have been injured and also concentrated during dam passage. Merrell (1961) observed a white sturgeon eating steelhead (*O. mykiss*) and chinook salmon (*O. tshawytscha*) which, he thought, were injured as they passed through an industrial plant on the Willamette River in Oregon. Concentrations of white sturgeon in dam tailraces increase their vulnerability to exploitation by bank anglers. Existing sanctuaries in dam tailraces provide significant conservation benefits to white sturgeon populations by restricting access by boat anglers to concentrations of sturgeon which are vulnerable to harvest.

Downstream from each dam, white sturgeon densities generally decreased as conditions became less riverine. The pattern in which white sturgeon moved downstream in summer and upstream in fall was reported by Haynes *et al.* (1978) in a study on the unimpounded Columbia River upstream of the McNary Dam Reservoir (Lake Wallula), and by Bajkov (1951) downstream of study reservoirs.

We caught white sturgeon at all depths, but observed little difference in catch rates at depths greater than 10 m. Although the low catch rates at depths less than 10 m in all reservoirs imply that white sturgeon prefer deep water, we took too few shallow water samples to confirm this preference. Fishers report good seasonal catches from shallow water flats with mussel beds. Additional work is

needed to evaluate depth preferences and their interactions with current velocity and substrate preferences.

White sturgeon moved long distances over relatively short time periods in each reservoir. Frequent movements of marked fish indicate they were well mixed in each reservoir, minimizing the chance for biases due to marking and recapture (Ricker 1975). Dams constrain movements of most white sturgeon, although a few passed a dam. Most dam passage was downstream rather than upstream. Although distribution of our sampling efforts made observations of downstream movements more likely than upstream movements, we saw virtually no upstream passage of dams by white sturgeon we tagged or of any of the thousands of fish tagged annually by fishery managers monitoring the sturgeon population downstream of Bonneville Dam. Avenues for downstream passage include fishladders, spillways, turbines, or navigation locks. Opportunities for upstream movements are limited to navigation locks or fish ladders which were designed for salmonids and rarely permit sturgeon to pass.

The minimal downstream movement from one reservoir to another is likely to have little effect on population size or productivity, either up- or downstream of the dam passed. However, this movement may prevent genetically different populations from developing in each pool. Even minimal immigration is sufficient to prevent genetic differentiation unless there is strong differential selection in different areas (Nei 1987). Divergence depends on the number of migrants entering a population, not their proportion (Allendorf and Phelps 1981). Relatively few migrants are needed to counteract the effects of genetic drift in large populations. The white sturgeon movements we observed are inconsistent with observations of genetic diversity among white sturgeon

populations in Bonneville, The Dalles, and John Day reservoirs based on differences in mitochondrial DNA (Brown *et al.* 1992). Larger sample sizes than used by Brown *et al.* (1992) may be required to accurately characterize differences.

White sturgeon evolved in a river environment characterized by diverse habitats corresponding to the surrounding topography and dynamic seasonal changes in prey abundance. The species appears to have adopted a nomadic life history strategy, in response to these conditions. This behavior persists in white sturgeon populations in the free-flowing section of the river downstream of Bonneville Dam (Bajkov 1951).

Dams are barriers to sturgeon movements and have created a series of populations which are functionally, if not genetically, discrete. Fish restricted to a reservoir cannot range among widely scattered habitats nor take advantage of seasonal concentrations of prey. Each population must depend on conditions within a specific reservoir to sustain produc-

tion. Dams appear to provide optimal conditions only in small areas (BRZ's) and result in a net reduction in habitat quality. Impoundment has reduced habitat diversity by creating a homogenous slack-water habitat which may not furnish optimal conditions for the white sturgeon life cycle in all years. The combination of reduced habitat diversity and constraints on movement may reduce white sturgeon productivity in the impounded portions of the river.

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Literature Cited

- Allendorf, F. W., and S. R. Phelps. 1981. Use of allelic frequencies to describe population structure. *Can. J. Fish. Aq. Sci.* 38:1507-1514.
- Anders, P. J., and L. G. Beckman. 1992. Location and timing of white sturgeon spawning in three Columbia River impoundments. In R. C. Beamesderfer and A. A. Nigro (eds.) Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam. Bonneville Power Administration. Pp. 47-60.
- Bajkov, A. D. 1951. Migration of the white sturgeon (*Acipenser transmontanus*) in the Columbia River. *Oreg. Fish Comm. Res. Briefs* 3:8-21.
- Beamesderfer, R. C., and B. E. Reman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Trans. Am. Fish. Soc.* 120:439-447.
- Brown, J. R., A. T. Beckenbach, and M. J. Smith. 1992. Influence of Pleistocene glaciations and human intervention upon mitochondrial DNA diversity in white sturgeon (*Acipenser transmontanus*) populations. *Can. J. Fish. Aq. Sci.* 49:358-367.
- Cochnauer, T. G., J. R. Lukens, and F. E. Partridge. 1985. Status of white sturgeon, *Acipenser transmontanus*, in Idaho. In F. P. Binkowski and S. I. Doroshov (ed.) North American sturgeons: biology and aquaculture potential. Dr. W. Junk, Dordrecht, The Netherlands. Pp. 127-133.
- Elliott, J. C., and R. C. Beamesderfer. 1990. Comparison of efficiency and selectivity of three gears used to sample white sturgeon in a Columbia River Reservoir. *Calif. Fish and Game* 76:174-190.
- Haynes, J. M., and R. H. Gray. 1981. Diel and seasonal movements of white sturgeon, *Acipenser transmontanus*, in the mid-Columbia River. *Fish. Bull.* 79:367-370.
- Haynes, J. M., R. H. Gray, and J. C. Montgomery. 1978. Seasonal movements of white sturgeon (*Acipenser transmontanus*) in the Mid-Columbia River. *Trans. Am. Fish. Soc.* 107:275-280.
- Merrell, T. R. 1961. Unusual white sturgeon diet. *Oreg. Fish Comm. Res. Briefs* 8:77.
- Nei, M. 1987. Genetic divergence and molecular phylogeny. In N. Ryman and F. Utter (ed.) Population genetics and fishery management, University of Washington Press, Seattle. Pp. 193-224.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Bd. Can. Bull.* 191.
- SAS. 1988a. Procedures guide; version 6.03 edition. SAS Institute, Cary, North Carolina.
- SAS. 1988b. User's guide; version 6.03 edition. SAS Institute, Cary, North Carolina.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. *Fish. Res. Bd. Can. Bull.* 184.
- Smith, G. E. 1978. An evaluation of disc-dangler tag shedding by striped bass (*Morone saxatilis*) in the Sacramento-San Joaquin estuary. *Calif. Fish and Game* 64(2):93-97.

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Do Edge Effects Influence Tree Growth Rates in Douglas-fir Plantations?

Abstract

Patch size and edge structure are known to influence microclimate, forest dynamics, and other ecological properties within forest fragments. Little is known about the nature of such "edge effects" within young plantations embedded in a matrix of older forest. Here we test the hypothesis that the growth rates of young Douglas-fir trees are reduced near the edges of plantations due to shading effects from adjacent forests. This hypothesis was examined in a single plantation where light levels were thought to be substantially reduced on the southern edge due to shading from a neighboring stand. Density of all trees and the heights and diameters at breast height (dbh) of artificially-regenerated Douglas-fir trees were measured along three parallel transects that extended 120 m into the plantation from its southern edge. We found that both tree height and dbh were significantly related to distance from the plantation edge when the effects of tree density were controlled for. Tree size was lower at 20 m from the edge than at all distances further from the plantation edge. These results suggest that the hypothesis merits additional testing with a replicated design across a range of environmental settings. The negative edge effect of tree growth reported here has implications for the design of plantation size, especially where small "gap" cuts are used.

Introduction

Several ecological processes in forest patches are known to be influenced by patch size and edge structure including: disturbance rates (Franklin and Forman 1987); decomposition (Klein 1989); nutrient cycling (Ryszkowski 1992); pollination (Jennersten 1988); and predation (Gates and Gysel 1978). Most studies have focused on forest fragments bordered by early successional vegetation. In Douglas-fir (*Pseudotsuga menziesii*) forests in the Pacific Northwest (PNW) United States, Chen (1991) found that many microclimatic variables were more extreme in forest edges than in forest interiors including wind velocity, solar radiation, soil temperature, and relative humidity. These edge effects extended 60-240 m into old-growth Douglas-fir stands (Chen *et al.* 1990). Vegetation structure and growth often vary along such microclimate gradients (Ranney *et al.* 1981, Kuppers 1992). The growth rates of both Douglas-fir and western hemlock (*Tsuga heterophylla*) were higher within 60 m of the forest edge than further into the forest (Chen *et al.* 1992). Such findings have focused much attention on the ecological consequences of forest fragmentation (Burgess and Sharp 1981, Harris 1984, Franklin and Forman 1987).

Considerably less is known about edge effects in early successional patches surrounded by forests of taller stature. Ryszkowski (1992) found in agri-

cultural fields adjacent to shelter belts that wind velocity and potential evapotranspiration were reduced, and that rainfall and crop yield were elevated, within 4-8 tree heights of the shelter belt compared with areas further into the field. Similarly, Chen (1991) reported that the edges of recent clearcuts had lower wind velocity, soil temperature and solar radiation (and higher soil moisture and humidity) than in the interiors of the clearcuts. In clearcuts in southwestern Oregon, Emmingham and Waring (1974) documented a steep gradient in solar radiation perpendicular to forest edges. Daily incident radiation and leader growth of Douglas-fir seedlings reached an asymptote between 4-21 m from forest edges of 12-25 m in height.

Knowledge of edge effects is likely important in the design of forest plantations. Harvest unit size, orientation, and edge structure may influence microclimate, vertebrate suitability, forest productivity, and other factors. For example, the growth rates of shade-intolerant tree species such as Douglas-fir may be reduced in a wide band along the south side of plantations due to shading from adjacent forests. Depending on the height and orientation of the forest edge, shading at some times of day may extend over 100 m into a plantation at the latitudes of western Oregon. Soil moisture in this zone, on the other hand, may be relatively favorable for tree growth. A better understanding of microclimate and tree growth along the gradient from patch edge to interior is likely to help forest managers to design plantations that best achieve goals for forest structure and productivity.

¹Present Address: Biology Department, Montana State University, Bozeman, MT 59717.

²Present Address: National Taiwan University, Taipei, Taiwan.

We conducted a case study of tree growth rates from the edge to the interior of a Douglas-fir plantation in western Oregon. Our goal was to test the hypothesis that Douglas-fir growth rates are inhibited on the shaded south edges of plantations surrounded by forest. We also wished to determine the width of the response zone. Only one study site was used in this initial test of the hypothesis. The location and edge orientation of the site were selected to maximize the effects of shading, minimize the effects of soil moisture, and thus to maximize negative edge effects on tree growth. We reasoned that if the hypothesis was rejected here, further study would not be warranted.

Methods

The study site was a 40 ha Douglas-fir plantation in the west central Oregon Coast Range, 9 km east of the Pacific Ocean and 13 km southeast of Newport, Oregon. This location is on the eastern edge of the *Picea sitchensis* vegetation zone (Franklin and Dyrness 1973) with the natural forest dominated by Douglas-fir, western hemlock, and Sitka spruce (*Picea sitchensis*). The maritime climate is mild and wet with frequent summer fog. The plantation is on a west-northwest facing slope of 15-30%, and a mean elevation of 150 m. The site was clearcut in 1979, treated with herbicides, and planted in 1980 (1046 trees/ha) and 1981 (592 trees/ha) with Douglas-fir, western red-cedar (*Thuja plicata*), western hemlock, and Sitka spruce. Natural regeneration occurred, subsequently resulting in variable tree densities across the plantation. The south side of the stand is bordered by a natural mature forest. The edge between these stands is straight, with a bearing of 283 degrees. Canopy trees on the edge are approximately 45 m in height.

Three parallel transects were established perpendicular to the south edge of the plantation. The transects were 80 m apart and extended 120 m into the plantation. Trees were sampled at 20-m intervals along the transects in 4 x 40-m plots that lay perpendicular to, and on east side of, the transects. Thus there was a total of 3 sample plots at each 20-m distance interval. Density of all trees (> 2 cm diameter at breast height, dbh) was determined by counting all stems in the sample plots. The height and dbh of planted Douglas-fir trees were determined by measuring 5-8 randomly selected Douglas-firs in each sample plot using a dbh tape and calibrated height pole. Planted trees

were identified by the vexar tubing (used at planting for protection from animal damage) that remained at their bases. Planted trees were chosen for study because they were known to be of similar age (hence we knew that tree size was due to factors other than age). Measurements were done only on Douglas-firs because sample sizes for other species were too few to allow for analysis.

The data were analyzed by determining mean density, height and dbh for each sample plot and then using plot means as the units of analysis. Height and dbh of the planted trees were used as indices of tree growth rates. Tests of normality indicated that height, dbh and total density (after a log transformation) did not differ significantly from the normal distribution. Analysis of variance was used to determine the relationships among independent variable, distance class from plantation edge, and the dependent variables tree density, dbh, and height. Additionally, analysis of covariance was used to control for the effect of tree density on the two tree size variables (height and dbh). Where significant differences were found, multiple range tests (Least Significant Difference Test, SAS 1982) were used to determine the distance intervals that differed from one another. The estimates of variance reported here are pooled estimates of standard error, which is desirable because of the assumption of homogeneity of variance that is made in the analysis of variance procedure.

Results

Tree density was not significantly related to distance from edge ($DF = 5,12$; $F = 0.40$; $P < 0.84$) (Figure 1). Height of planted tree was also not significantly related to distance from edge ($DF = 5,12$; $F = 1.19$; $P < 0.37$). Planted tree height was correlated with total tree density ($n = 18$; $r = .50$; $P < 0.03$). Controlling for the effect of density, planted tree height was significantly lower at the 20-m distance class than at all others ($DF = 6,11$; $F = 3.04$; $P < 0.054$) (Figure 2). No differences were found among the other distance classes.

Dbh of planted trees was not correlated with total tree density ($n = 18$, $r = 0.36$; $P < 0.13$). This variable was weakly related with distance from edge when not controlling for density ($DF = 5,12$; $F = 2.8$; $P < 0.067$) and when controlling for density ($DF = 6,11$, $F = 4.45$; $P < 0.016$) (Figure 3). Only the 20-m distance class differed significantly from the others.

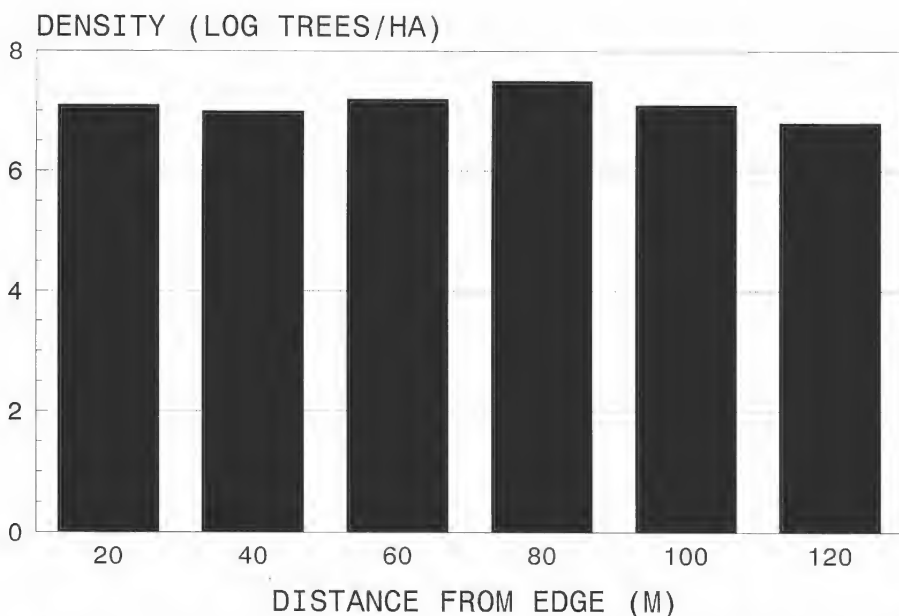


Figure 1. Mean tree density (under a log transformation) in a Douglas-fir plantation along a gradient from plantation edge to interior. The pooled standard error for the samples was 0.32.

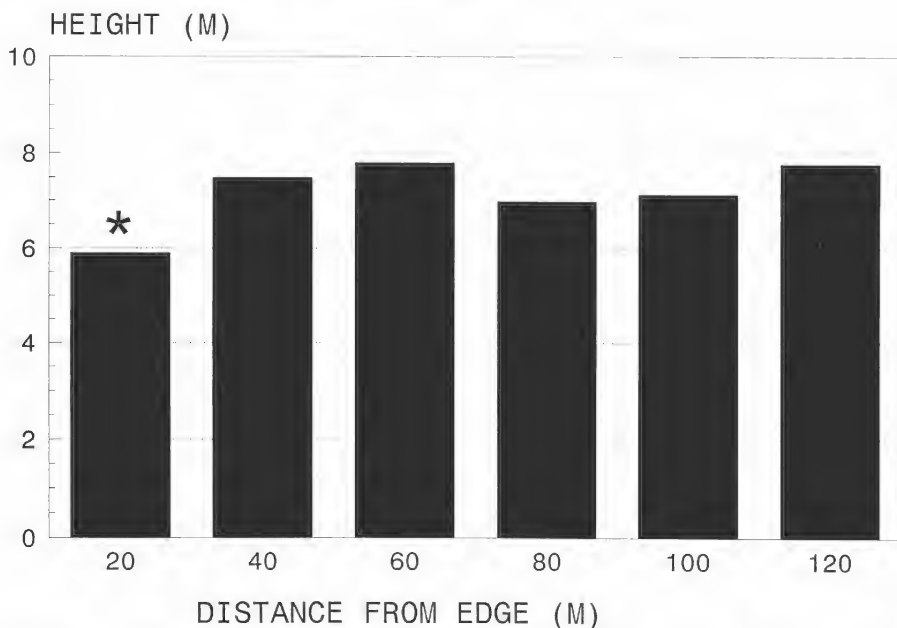


Figure 2. Mean height (controlling for log tree density) of planted Douglas-fir trees along a gradient from plantation edge to interior. "*" denotes that the distance class differs significantly from all others. The pooled standard errors for the samples ranged from 0.483 to 0.510.

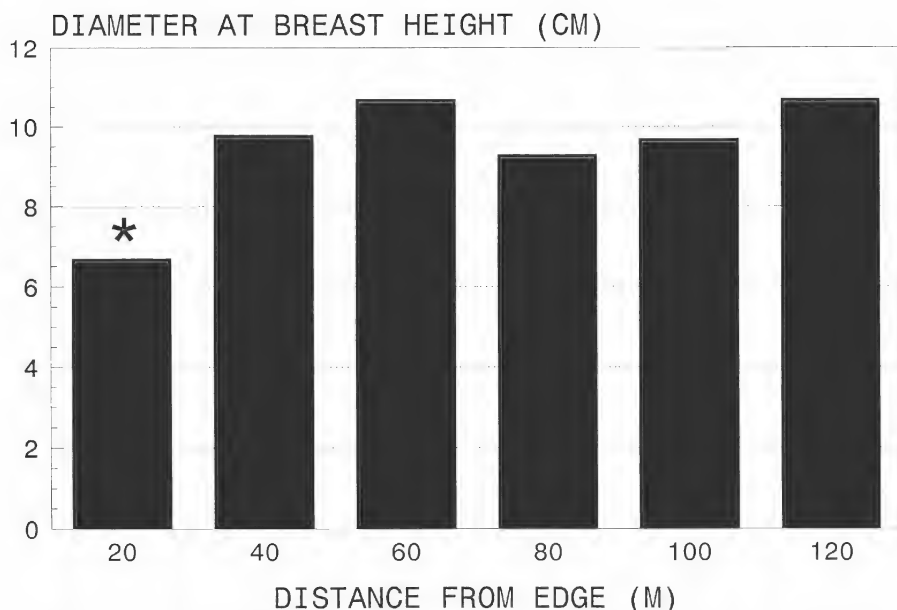


Figure 3. Mean dbh (controlling for log tree density) of planted Douglas-fir trees along a gradient from plantation edge to interior. "*" denotes that the distance class differs significantly from all others. The pooled standard errors for the samples ranged from 0.711 to 0.740.

Discussion

The results indicated that total tree density influenced the growth rates of the Douglas-fir trees. Natural regeneration caused tree density to be variable across the study area. This necessitated controlling for the effect of density in assessing the relationship between tree growth and distance from edge.

When density was controlled for, both the height and dbh of Douglas-fir trees were significantly depressed at 20 m from the stand edge. This effect was not observed further from the edge. It is difficult to explain these results with certainty without microclimate measurements. One possibility is that light is the primary limiting factor and that light levels were sufficient at distances ≥ 40 m from the shaded edge to allow maximum Douglas-fir growth. This explanation is consistent with the findings of Emmingham and Waring (1974). An alternative possibility is that these trees are also limited by soil moisture. Soil moisture is elevated near the shaded edge (Chen 1991), and the abundance of this resource may mask the effect

of shading on tree growth at distances of 40 and 60 m.

The fact that the study site has a maritime climate with extensive fog during the growing season may have bearing on each of these possibilities. The shading effect of the mature forest edge would not occur on cloudy or foggy days (Chen 1991). Hence the effects of shading may be less at this site than further inland where direct radiation occurs on more days of the growing season. Maritime conditions also make it less likely that soil moisture deficits inhibit tree growth at the site. Replicated analyses at other sites representing a range of environmental conditions is needed to better understand the role of edge effects in plantations.

The results of this study indicate that in the study area the negative edge effects on tree growth are restricted to a relatively narrow band along even the most shaded side of a plantation. This finding becomes increasingly relevant where small "gap" cuts are used to balance wood production

and habitat goals. Assuming negative edge effects only within a 20-m band on the south side of square harvest units, patches 40, 80, and 160 m on a side would experience reduced growth over 50%, 25% and 12% of their areas, respectively.

Acknowledgments

We thank William Emmingham, Tom Sabin, and two anonymous reviewers for comments on the

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Literature Cited

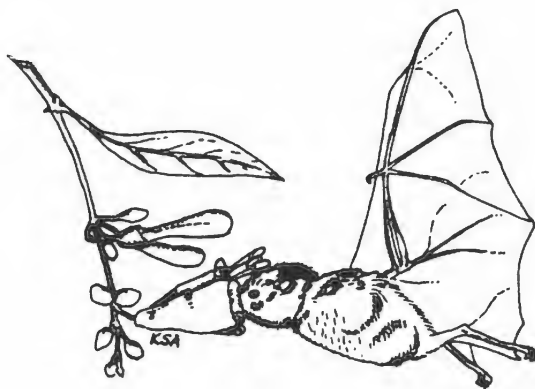
- Burgess, R. L., and D. M. Sharp, eds. 1981. *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York.
- Chen, J. 1991. Edge effects: microclimatic pattern and biological responses in old-growth Douglas-fir forests. Ph.D. Diss., University of Washington, Seattle, WA, USA.
- Chen, J., J. F. Franklin, and T. A. Spies. 1990. Microclimatic pattern and basic biological responses at the clearcut edges of old-growth Douglas-fir stands. *Northw. Env. J.* 6:424-425.
- . 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Appl.* 2(4):in press.
- Emmingham, W. H. and R. H. Waring. 1974. Conifer growth under different light environments in the Siskiyou Mountains of southwestern Oregon. *Northw. Sci.* 47(2):88-99.
- Franklin, J. F. and C. T. Dyrness. 1973. *Natural Vegetation of Oregon and Washington*. USDA Forest Service, Pacific Northw. For. and Range Exp. Sta., Portland, Oregon.
- Franklin, J. F. and R. T. Forman. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. *Landscape Ecol.* 1:5-18.
- Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. *Ecol.* 59:871-883.
- Harris, L. D. 1984. *The Fragmented Forest*. University of Chicago Press, Chicago, Illinois.
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia Brazil. *Ecol.* 70(6):1715-1725.
- Jennersten, O. 1988. Pollination in *dianthus-deltoides* caryophyllaceae effects of habitat fragmentation on visitation and seed set. *Cons. Biol.* 2(4):359-366.
- Kuppers, M. 1992. Changes in plant ecophysiology across a central European hedgerow ecotone. In A. J. Hansen and F. di Castri (eds.), *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer Verlag, New York. Pp. 285-303.
- Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. In Burgess, R. L. and D. M. Sharpe (eds.), *Forest Island Dynamics in Man-dominated Landscapes*. Springer-Verlag, New York. Pp. 67-96.
- Ryszkowski, L. 1992. Energy and material flows across boundaries in agricultural landscapes. In A. J. Hansen and F. di Castri (eds.), *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer Verlag, New York. Pp. 270-284.
- SAS. 1982. *SAS User's Guide: Statistics*. SAS Institute Inc., Cary, North Carolina.

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**PROGRAM AND ABSTRACTS OF THE
NORTHWEST SCIENTIFIC ASSOCIATION
66th Annual Meeting**

**Held in Conjunction With:
THE INLAND CHAPTER OF THE
SOCIETY FOR NORTHWESTERN VERTEBRATE BIOLOGY
and
THE NORTHWEST LICHEN GUILD**



**March 24-27, 1993
Eastern Oregon State College
La Grande, Oregon**

SCHEDULE OF EVENTS

Wednesday, March 24

7:00-9:00 pm Registration and Social
8:00-10:00 pm Board of Trustees Meeting

Thursday, March 25

8:00-4:30 Registration
8:00-4:30 Wildlife Art Show
8:00-5:30 SYMPOSIUM: Forest Health Issues; Co-sponsored by the Blue
 Mountain Natural Resources Institute and the Pacific
 Northwest Research Station
8:00-5:30 SYMPOSIUM: Research and management of bats in the Northwest
8:30-10:30 CONTRIBUTED PAPERS: Aquatic Biology
10:50-4:30 CONTRIBUTED PAPERS: Botany
8:50-10:30 CONTRIBUTED PAPERS: Geology
12:00-1:30 NSWA Business Lunch (included in registration fee)
1:30-4:00 Lichen Workshop
6:30-9:00 NSWA banquet, Jack Ward Thomas, Speaker

Friday, March 26

8:00-12:00 Registration
8:00-12:00 Wildlife Art Show
8:00-4:40 SYMPOSIUM: Cumulative effects of land management practices on
 anadromous salmonids
8:50-3:30 CONTRIBUTED PAPERS: Ecology
8:30-12:00 CONTRIBUTED PAPERS: Forestry
8:50-11:00 CONTRIBUTED PAPERS: Lichens and Mosses
12:00-1:30 Lunch
1:30-3:10 CONTRIBUTED PAPERS: Zoology
1:30-5:00 Field Trips:
 Starkey Experimental Forest
 Forest Health in Northeast Oregon

Saturday, March 27

9:00-4:00 Field trips:
 Geology of the Grande Ronde Valley (9:00-12:00)
 Salmonid Ecology (9:00-4:00)
 Forest Lichens, Anthony Lakes (9:00-2:30)

SYMPOSIUM: FOREST HEALTH ISSUES

Thursday, March 25

Co-sponsors: Northwest Scientific Association
Blue Mountain Natural Resources Institute
Pacific Northwest Research Station

INTRODUCTION: CURRENT SITUATION IN BLUE MOUNTAINS, ACRES AFFECTED, OWNERSHIPS, RESOURCES, RESEARCH, Tom Quigley, Director, Blue Mountains Natural Resources Institute, La Grande, OR.

BACKGROUND: ECOLOGIC/CLIMATIC/FOREST TYPES/ROLE OF FIRE, Charlie Johnson, Area Ecologist, Wallowa-Whitman National Forest, Baker City, OR.

ROLE OF DEFOLIATORS:

RESEARCH ON BUDWORM, TUSsock MOTH, HISTORICAL PERSPECTIVES, TREE GROWTH AND MORTALITY, Boyd Wickman, Research Entomologist, Pacific Northwest Research Station, La Grande, OR.

MANAGEMENT: SILVICULTURE, AERIAL SPRAYING, MONITORING, Dave Overhulser, Entomologist, Oregon Department of Forestry, Salem, OR.

CHARACTERISTICS OF LOGS UTILIZED BY ANTS IN PILEATED WOODPECKER HOME RANGES IN NORTHEASTERN OREGON, Torolf Torgersen, Research Entomologist and Evelyn Bull, Research Wildlife Biologist, Pacific Northwest Research Station, La Grande, OR.

ROLE OF BARK BEETLES:

RESEARCH ON MOUNTAIN PINE BEETLE, DOUGLAS-FIR BEETLE, OTHER BEETLES, HISTORICAL PERSPECTIVES, TREE MORTALITY, Darrell Ross, Assistant Professor of Integrated Forest Protection, Oregon State University, Corvallis, OR.

MANAGEMENT: SILVICULTURE, MONITORING, Paul Flanagan, Zone Entomologist, Wenatchee National Forest, Wenatchee, WA.

ROLE OF PATHOGENS:

RESEARCH ON ROOT DISEASES, STEM DECAYS, DWARF MISTLETOES, HISTORICAL PERSPECTIVES, TREE GROWTH AND MORTALITY, Greg Filip, Associate Professor of Integrated Forest Protection, Oregon State University, Corvallis, OR.

MANAGEMENT: SILVICULTURE, MONITORING, Alan Kanaskie, Forest Pathologist, Oregon Department of Forestry, Salem, OR.

EFFECTS OF CLIMATIC STRESS ON FOREST HEALTH: DROUGHT STRESS ON HOSTS, DEFOLIATORS, PATHOGENS, Catherine Parks, Plant Pathologist, Pacific Northwest Research Station, La Grande, OR.

POLICY ON SALVAGE/SILVICULTURE/REHABILITATION, Jeff Blackwood, Forest Supervisor, Umatilla National Forest, Pendleton, OR.

SYMPOSIUM:
RESEARCH AND MANAGEMENT OF BATS IN THE NORTHWEST

Thursday, March 25

OPENING COMMENTS, Burr Betts, Dept. of Biology, Eastern Oregon State College, La Grande.

LINKING BAT ACTIVITY WITH LANDSCAPE-LEVEL ATTRIBUTES USING GIS, Mark Huff, John Lehmkuhl, and John Young, USDA Forest Service, Pacific Northwest Research Station, Olympia, WA.

BAT ACTIVITY IN MANAGED FORESTS OF THE SOUTHWESTERN CASCADE RANGE, Janet Erickson, College of Forest Resources, Univ. of Washington, Seattle.

BAT DIVERSITY AND HABITAT USE IN A MANAGED FOREST, Lori Campbell, Dept. of Natural Resources, Washington State Univ., Pullman.

THE THERMAL IMPLICATIONS OF ROOST SITE SELECTION IN HIBERNATING *PLECOTUS TOWNSENDII*, Bill Doering, Dept. of Biology, Idaho State Univ., Pocatello.

CHARACTERISTICS OF WINTER ACTIVITY IN *PLECOTUS TOWNSENDII* IN SOUTHEASTERN IDAHO, Bill Bosworth, Dept. of Biology, Idaho State Univ., Pocatello.

MONITORING BAT USE OF OLD GROWTH REDWOOD FORESTS: PRELIMINARY RESULTS AND A PROPOSAL FOR FUTURE WORK, Steve Gellman and Bill Zielinski, USDA Forest Service, Northern Redwoods Laboratory, Arcata, CA.

SOME APPLIED ASPECTS OF BAT RESEARCH IN SOUTHERN OREGON, Steve Cross, Biology Dept., Southern Oregon State College, Ashland.

INVESTIGATIONS AND MANAGEMENT OF TOWNSEND'S BIG EARED BATS (*PLECOTUS TOWNSENDII*) IN HELL'S CANYON NATIONAL RECREATION AREA, Ralph Anderson, USDA Forest Service, Wallowa Valley Ranger District, Enterprise, OR.

IMPLICATIONS AND BENEFITS OF LONG-TERM BAT MONITORING IN NATIONAL FORESTS, Mark Perkins, Portland, OR.

SURVEY PROTOCOL AND AN INTERIM SPECIES CONSERVATION STRATEGY FOR *PLECOTUS TOWNSENDII*, Tim Schommer, USDA Forest Service, Wallowa-Whitman National Forest, Baker City, OR. and Mark Perkins, Portland, OR.

CHANGING THE LOOK OF HIGH SCHOOL BIOLOGY. CAN STUDENTS DO BATS?, Stuart Perlmeier, Pat Greenlee, Aimee Hart, and Jesse Fittipaldi, York University, Willamette National Forest and Springfield High School, Eugene, OR.

CLOSING COMMENTS, Burr Betts, Dept. of Biology, Eastern Oregon State College, La Grande.

SYMPOSIUM:
CUMULATIVE EFFECTS OF LAND MANAGEMENT PRACTICES
ON ANADROMOUS SALMONIDS

Friday, March 26

Research on Elements of Cumulative Effects:

HISTORICAL CHANGES IN ANADROMOUS FISH HABITAT IN THE UPPER GRANDE RONDE RIVER BASIN, Bruce McIntosh and Sharon E. Clarke, Oregon State University, Corvallis, James R. Sedell, Pacific Northwest Research Station, Corvallis.

SEDIMENT DELIVERY TO HEADWATER STREAM CHANNELS FOLLOWING TIMBER HARVEST IN THE UPPER GRANDE RONDE RIVER, Robert Gill, USFS, Wallowa-Whitman National Forest, La Grande, Harry A. Froehlich, Oregon State University, Corvallis.

SUMMER STREAM TEMPERATURES IN THE UPPER GRANDE RONDE RIVER BASIN - A PRELIMINARY REPORT, Todd Bohle, Department of Forest Engineering, Oregon State University, Corvallis.

RIPARIAN AREA VEGETATION ASSESSMENT AND RECOVERY, Doug Green, Arizona State University.

Taking Research to Management Implementation:

THE PACFISH EFFORT, James Sedell, Pacific Northwest Research Station, Corvallis, OR.

WATERSHED CUMULATIVE EFFECTS? THE UPPER GRANDE RONDE FISH HABITAT PROTECTION, RESTORATION, AND MONITORING PLAN. John Anderson, Wallowa-Whitman National Forest, Baker City, OR.

THE USFS' UNSOUND PROCEDURE FOR DETERMINING THE CUMULATIVE EFFECTS OF LAND-USE ON SALMON AND AN ALTERNATIVE APPROACH: "ENOUGH IS ENOUGH," Jonathan J. Rhodes, Columbia River Inter-Tribal Fish Commission, Portland, OR.

Panel Discussion: Cumulative Effects and Policy Implementation:

PANEL FACILITATOR: Jeff Zake, Oregon Department of Fish and Wildlife, La Grande.

PANEL MEMBERS:

Glen McDonald, Wallowa-Whitman National Forest, Enterprise, OR.

Ron Wiley, Bureau of Land Management, Portland, OR.

Michael Tehan, National Marine Fisheries Service, Portland, OR.

Jim Lauman, Oregon Department of Fish and Wildlife, La Grande, OR.

Unnamed representative, Confederated Tribes of the Umatilla Indian Reservation, Pendleton, OR.

1

INVESTIGATIONS AND MANAGEMENT OF TOWNSEND'S BIG-EARED BATS (*Plecotus townsendii*) IN HELL'S CANYON NATIONAL RECREATION AREA. Ralph G. Anderson, USDA FS, Wallowa Valley Ranger District, Enterprise.

The US Forest Service, Hell's Canyon National Recreation Area is actively implementing many management activities in and around a significant sub-population of Townsend's big-eared bat (*Plecotus townsendii*), along the Snake River canyon and surrounding area. The National Forest Management Practices Act of 1976 and the Hell's Canyon National Recreation Area Designation Act of 1972, both charge integral accountability for endemic species. The several agencies sharing accountability have been active in surveying for and management on behalf of Townsend's big-eared bats. These efforts have included survey, radio-telemetry, assessment, installation of protective gates and interpretation. Some of the impetus for management has come from the US Fish and Wildlife Service listing of the species as a candidate for threatened or endangered listing (C2). Attention to the estimated three hundred and fifty animals is on-going.

2

DEVELOPING NEW PESTICIDES IN A CHANGING WORLD. Leonard R. Askham, Washington State University, Pullman, WA.

The public's concern and political pressure to reduce or eliminate pesticide use in agriculture has been a growing phenomenon. During the last decade a number of pesticides were removed from the market and several more appear to be headed for the same fate. The reasons are numerous but the overriding factor is that the public perceives them to be dangerous and no amount of breast beating and expert testimony will change their minds. This paper, based on the experience of developing and registering a biochemical pesticide, addresses the questions about how alternatives may likely be developed in the future and which sectors of society will pay for them.

3

FIVE YEARS OF DATABASEING AT THE INTERMOUNTAIN HERBARIUM: LESSONS, PROGRESS, AND PROBLEMS. Mary E. Barkworth, Utah State University, Logan, Utah 84322-5305.

When we first decided to start databasing the information in the Intermountain Herbarium, we had two primary goals: 1) Efficient label preparation and 2) Rapid information retrieval. These are still our primary goals, but we are less ambitious in terms of what information we expect to be able to retrieve. On the other hand we have added a third goal, facilitating computer preparation of distribution maps. Lesson no. 1? It is best to have a program that someone locally can work with, usually a permanent herbarium employee. Corollary: Select the basic program in accordance with the time and ability of that employee (at UTC it is me; the program we use is Alpha4 which is designed for non-programmers). The value of a database is almost completely dependent on the accuracy of the entries. The accuracy of the identification is by far the most important. There are no short cuts for achieving it. Accuracy of data entry for standardized information (e.g., scientific names, states, counties) can be ensured by using "Look up" tables. We have not found them useful in speeding up data entry. Lesson 2: Computerization does not necessarily save time in herbarium maintenance. Although we use the same program for entering label information as for the database, we now need to enter information from specimens received on exchange and to correct entries for annotated specimens. Before computerization, such specimens were filed directly. We now only enter specimens from west of the Mississippi. Development of the label writing program has been the most difficult task; I called on a colleague. For computer mapping, lat/long data are ideal, but not often provided; UTM data may be awkward if more than one zone is involved; township/range data cannot be used directly. We are currently exploring ways of translating township/range data to lat/long data.

4

SEDIMENTATION AND TECTONICS IN THE GRANDE RONDE GRABEN. Ellen Morris Bishop, Pacific Rivers Council, La Grande. Laura Thompson, Eastern Oregon State College, La Grande and Jeffery Woodward, University of Maine, Farmington

The Grande Ronde Valley is a pull-apart basin formed in response to dextral shear along the Olympic Wallowa Lineament. Its igneous, sedimentary, and tectonic histories are inter-related. Intermediate, post CRB (Grande Ronde) volcanic rocks, 13 Ma to 6.5 Ma rim and floor the graben; their mineralogy suggests their eruption was related to rifting. The Grande Ronde graben bedrock floor, buried beneath 400 to 500 m of sediments, is irregular on the order of tens to a hundred meters, indicating the persistence of small faults and multiple fault blocks between the major valley-bounding faults. These faults may be major pathways for deep artesian water circulation. The valley-filling sediments include laterally discontinuous gravels, sands, and reduced sandy clays. They indicate deposition in fluvial environments by vigorous stream transport and widespread overbank deposition. Wood recovered from 430 feet depth south of Island City was C14-dated at 33,000 years, suggesting especially rapid fluvial sedimentation in the late Pleistocene. Although no Recent fault-related offsets have been confirmed in or around the Grande Ronde valley, faults in the valley subsurface appear to confine meander loops of the Grande Ronde River and Catherine Creek, suggesting frequent low-intensity seismic activity during the late Pleistocene and Holocene.

FOREST HEALTH ISSUES IN THE BLUE MTS
Jeff D. Blackwood, Umatilla National
 Forest, Pendleton, Oregon.

Forest health issues in the Blue Mountains continue to challenge resource managers, communities, and a wide variety of people, organizations, and agencies with interests in the Blue Mountain ecosystems. Traditional approaches of resolving these issues have not been very effective on public lands. Ecosystem management processes need to be developed that focus on the future, deal with concepts of sustainability, and recognize the needs of society and economic realities. The Blue Mountains provide an outstanding opportunity for developing ecosystem restoration strategies where research plays a key role, and interested publics are more meaningfully involved in land management decisions. There is also a significant opportunity for neighboring landowners and managers to communicate their objectives, and cooperatively work toward accomplishing common needs. A system of monitoring and evaluating results of both land management practices and coordination efforts is needed.

SUMMER STREAM TEMPERATURES IN THE
 UPPER GRANDE RONDE RIVER BASIN
 (UGRRB) - A PRELIMINARY REPORT.
Todd S. Bohle, Oreg. State Univ.,
 Corvallis, Dr. Robert L. Beschta,
 Oreg. State Univ., Corvallis.

Evaluating patterns of summer stream temperatures within the UGRRB may serve as an index of the relative health of riparian systems. Our objective was to identify patterns in summer stream temperatures and factors which influence them within the UGRRB. Hourly minimum, maximum, and average stream temperatures were collected at 30 sites along the mainstem and tributaries during the summers of 1991 and 1992. Maximum summer stream temperatures within the mainstem of the Grande Ronde River averaged 75.8°F (23.1°C) and 78.4°F (23.9°C) in 1991 and 1992, respectively. Maximum stream temperatures >75°F were observed at 70% of the sites during the summer of 1992. Maximum stream temperatures occurred during August in both years and were commonly observed above the range known to be physiologically stressful to anadromous fish.

CHARACTERISTICS OF WINTER ACTIVITY IN
PLECOTUS TOWNSENDII IN SOUTHEASTERN
 IDAHO. William R. Bosworth and Barry L. Keller,
 Idaho State University, Pocatello, Idaho.

A colony of approximately 150 Townsend's big-eared bats (*Plecotus townsendii*) hibernating in a l. a-tube cave on the Idaho National Engineering Laboratory was evaluated weekly to determine relative frequencies of movement (RFM), the distribution of the colony within the cave, and the degree of social roosting. Activity near the mouth of the cave was monitored continuously for several days each month. Midwinter RFM's ranged from 0.05 to 0.13 movements per bat per day, the minimum occurring in mid-December. Individual movement patterns were not evident but overall colony distributions remained consistent throughout midwinter. Bat distribution was unimodal and skewed toward the back of the cave. Activity was evident at the mouth of the cave throughout the winter; daily event totals varied considerably. Circadian activity patterns were more evident during early hibernation than in midwinter. A maximum of 20% of the colony was roosting in clusters near the beginning of hibernation though more typically the rate was around 10%. Understanding winter behavior patterns of bats may be important when evaluating human disturbance to hibernating *Plecotus* populations.

AN EXAMINATION OF THE CYST
 MATURATION PERIOD OF *Giardia*
lamblia USING IN VITRO
 EXCYSTATION AND THE
 FLUOROGENIC DYES FLUORESCIN
 DIACETATE AND PROPIDIUM
 IODIDE. Richard P. Bradley, Central
 Washington University, Ellensburg.

Giardia lamblia is the most frequently identified waterborne pathogenic protozoan in the United States. The methods which have been used to determine the viability of *G. lamblia* have included dye exclusion, and in vitro excystation. It has been reported that *Giardia* cysts require a maturation period from 2 to 7 days before reaching full excystation potential. Cysts were examined using fluorogenic dyes and in vitro excystation over a period of 14 days. A maturation period does seem to be required to achieve full excystation and maximize fluorescein diacetate inclusion potential.

THE COSTS OF RESISTANCE TO PARASITISM IN AEDES SIERRENSIS. Leonard E. Broberg University of Oregon, Eugene.

Most models of parasite-host coevolution assume that there are costs to increased host resistance which constrain its evolution in the host. The host Aedes sierrensis, the western treehole mosquito, and its ciliate parasite, Lambornella clarki, were used to test this hypothesis. A. sierrensis and L. clarki may or may not co-occur in individual treeholes found throughout the Willamette Valley of Oregon. Mosquito hosts surviving to oviposit eggs in L. clarki infected treeholes have resisted parasitization. Pupae of the host mosquito were removed from three L. clarki infected holes and four L. clarki uninfected holes in the field to the laboratory. Females were reared in the lab and mated to randomly selected males. Fecundity increased with female size, but weight-specific fecundity did not differ between females from infected and uninfected holes. These results indicate that there is no cost to mosquito fitness of resistance to the protozoan parasite. This research was supported by a Northwest Science Association Student Research Grant.

STUNTED GROWTH IN TAILED FROG TADPOLES (ASCAPHUS) FROM A SUBALPINE POPULATION IN THE NORTH CASCADES. Herbert A. Brown, Western Washington University, Bellingham.

I collected tadpoles from a stream on slopes of Yellow Aster Butte (Whatcom County) at an elevation of 1500 m in July and September, and measured body weight and size (morphometric analysis of ten features). In July there are three groups: juveniles (hatched from eggs of the previous summer) with total length = 28.0 mm and body weight = 184 mg, 2-year tadpoles with 34.7 mm and 388 mg, and 3-year tadpoles (metamorphs) with 39.2 mm and 571 mg. In September the small (juvenile) tadpoles are 31.2 mm and 276 mg and the large (mature) tadpoles are 37.8 mm and 516 mg. Hatchlings of the current year probably leave the egg nest sites during October. Tadpole development requires three years: one embryonic summer, two larval summers, and a final metamorphic summer. The body size of these tadpoles is greatly reduced when compared to lowland populations where mature tadpoles are 52.6 mm and 1800 mg. Reduced food resources and low temperatures may retard the tadpole growth in this subalpine population.

PLANT COMPOSITION AND BIOMASS RESPONSE TO ORGANIC MATTER REMOVAL IN A PONDEROSA PINE FOREST. M.D. Busse and W.E. Hopkins, USDA Forest Service, Bend, Oregon.

Organic matter retention is an important component in the sustainability of managed forests. We tested the relationship between organic matter retention and plant productivity in second growth ponderosa pine stands of central Oregon. Four levels of organic matter removal following thinning were evaluated: remove whole trees; remove boles only; no removal; and no thinning. Prescribed underburning and fertilization were included in a factorial combination with each level of organic matter removal. Biomass equations for the dominant shrub species were developed based on canopy volume and stem diameter. Above-ground productivity was measured for all herbaceous species in the first year following treatment. Herbaceous biomass and species composition responded only to thinning and fertilization; no differences were found due to amount of organic matter removal or prescribed underburning.

QUANTIFYING HABITAT FRAGMENTATION IN FORESTED LANDSCAPES. Douglas R. Call, Lisa A. Nordstrom, James G. Hallett, Lori A. Campbell, Washington State University, Pullman, Margaret A. O'Connell, Eastern Washington University, Cheney.

Identifying the pattern and extent of habitat fragmentation is an essential first step to predicting effects of fragmentation on species diversity and population dynamics. Landsat satellite imagery (1991) for northeast Washington State was classified into four forest habitat types and converted into polygon maps with a 2 ha minimum mapping unit. We generated habitat maps for 20 watersheds (2,000-8000 ha) representing a range of fragmentation intensities from timber harvest activities. We estimated fractal dimensions for each habitat type and included these with several standard landscape measures in a principal components analysis (PCA). These results were unsatisfactory so we developed a random line-transect sampling method to estimate the probabilities of encountering changes in habitat types. The transect sampling appeared to be a better indicator of the degree of fragmentation.

NEST REMOVAL REDUCES REINVASION BY MOUNTAIN BEAVER (*Apodonta rufa*). Dan L. Campbell and James P. Farley, USDA, APHIS, ADC, Denver Wildlife Research Center, Olympia, WA.

Mountain beaver damage to tree crops is briefly reduced by trapping, but intact systems are rapidly reoccupied. After depopulation of a clearcut near Olympia, Washington, 15 intact systems and 15 systems with nests removed were compared with older unoccupied systems. Within 4 months, 67% of intact systems, 13% of systems with nests removed, and 0% of old systems were reoccupied. During 55 months, intact systems were occupied 61% of the time, systems with nests removed were occupied 29% of the time, and old systems were occupied 6% of the time. Average occupancy for intact systems was 33 months (SD 16 months), systems with nests removed 16 months (SD 17 months), and old systems 8 months (SD 14 months). The long term reduction of burrow occupancy may be enhanced by nest removal.

BAT DIVERSITY AND HABITAT USE IN MANAGED FORESTS. Lori A. Campbell, Washington State University, Pullman.

Better knowledge of bat life history and ecology are crucial for successful conservation of these species in human impacted environments. I examined the occurrence, diversity and habitat use of bats in a managed forest in the Selkirk Mountains of northeastern Washington. Bats were sampled using mist nets and Tuttle traps at stream and road sites. Captures included eight species (n=66), but not all species were represented at each capture site. One species, *Lasionycteris noctivagans*, was selected for an intensive study of roosting ecology using radio telemetry. A total of nine roost sites for six individuals were located within 3km of the initial capture site. All roosts were located in snags with exfoliating bark, extensive vertical cracks and/or cavities. Eight roosts were located in snags with diameter at breast height > 30 cm.

SOME APPLIED ASPECTS OF BAT RESEARCH IN SOUTHERN OREGON. Stephen P. Cross, Southern Oregon State College, Ashland.

Studies of bats in southern Oregon and northern California during the last several years have yielded findings of potential value for future study and management. Radio-tracking Townsend's big-eared bat (*Plecotus townsendii*) during late summer and fall, 1991 and 1992 in the Klamath River Canyon, shows patterns of local use of temporary locations. Attempts to find a major unknown hibernation site were unsuccessful but produced useful information. Determination of seasonal use patterns of a maternity roost indicates significant year-to-year variation which must be considered when employing seasonal site protection. Radio-tracking of a pallid bat (*Antrozous pallidus*) led to the discovery of a heretofore unknown type of roost site. Field and lab tests of bat boxes are underway. Preliminary evidence suggests that both design characteristics and placement selection are important for attracting bats. Species specific methods of counting bats have been employed. Photographic methods show some promise both inside and outside of roost sites.

CHARACTERIZATION OF LOESS DEPOSITS AT THE INEL, IDAHO. Thomas V. Dechert, and Paul A. McDaniel, University of Idaho, Moscow.

Loess occurs throughout the Pacific Northwest, especially at lower elevations and on gentle slopes. The distribution and characteristics of the various loess deposits can be used to develop an understanding of landscape evolution. We characterized the loess deposits occurring around the Idaho National Engineering Laboratory (INEL) Radioactive Waste Management Complex to better understand the landscape dynamics of the area relative to the fate of stored radioactive wastes. In addition to normal soil characterization analyses, we developed signature particle size distribution curves for the loessal silts and fine sands. Using a Coulter Counter TAIL, silts are subdivided into 15 size classes. Sands are sieved into 11 classes. Different loess deposits can be identified based on curve shapes. When associated with other soil characteristics and landscape information, different loess deposits can be correlated to probable times of deposition and episodes of soil formation. The resulting stratigraphic relationships are used to assess landscape evolution and stability.

LICHEN RESPONSES TO MANIPULATION. William C. Denison, Oregon State University, Corvallis.

When lichens are subjected to experimental treatment they react. A response may be immediate (seconds) or take days, weeks, or months. Some responses are evident to the naked eye; others are only detected with the help of instruments. A few responses are used commonly in experiments; others are not. Some of the little-used responses deserve more attention. Among these are: growth rate; production of asexual propagules; spore discharge and germination; rhizine production; anastomosis; and healing. Most of these can be seen and measured with the simplest of equipment, or with none at all. Most of them are important in the establishment and long term survival of the species. If we hope to manage lichen populations, we need to pay attention to a wide range of responses.

THE THERMAL IMPLICATIONS OF ROOST SITE SELECTION IN HIBERNATING *PLECOTUS TOWNSENDII*. Robert W. Doering and Barry L. Keller, Idaho State University, Pocatello.

Winter survival among hibernating animals is intimately coupled to the conservation of energy and materials. A first step in understanding the overall physiological ecology of hibernation is understanding the thermal relationship of an animal with its environment. To evaluate the thermal energetics of hibernating *Plecotus townsendii* under natural conditions, we monitored environmental changes within natural lava-tube hibernacula and measured body temperatures (Tb) of free-ranging bats at the Idaho National Engineering Laboratory. A unique aspect of this study is the continuous monitoring of the physical environment using automated data acquisition systems. Tbs and body weights were obtained manually from selected bats throughout hibernation. Continuous monitoring of the physical environment has shown that hibernacula are more varied and dynamic than previously observed. Successful hibernacula have available temperatures below deep soil temperature. Single opening lava-tube hibernacula take the form of a two-dimensional thermal gradient. The hibernating population distributes itself across this gradient. Bats choose environmental temperatures (Te) between 2.5 C and 0.0 C, though higher temperatures are available. Tb seems closely linked to Te throughout the hibernation season.

COMMERCIAL THINNING AND UNDERPLANTING TO ENHANCE STAND STRUCTURAL DIVERSITY IN YOUNG DOUGLAS-FIR PLANTATIONS. William H. Emmingham and Gabriel F. Tucker, Oregon State University, Corvallis.

Within the millions of acres now designated as Habitat Conservation Areas in Western Oregon and Washington are hundreds of thousands of acres of young (0-30 years old) plantations of Douglas-fir. These dense, nearly-pure plantations develop into closed canopy forests and remain in that condition for decades.

Adaptive COPE OSU, PNW Experiment Station, and the Siuslaw National Forest are cooperating on a study to test the hypothesis that commercial thinning will hasten development of stand structure favorable to the spotted owl and its prey species. Treatments include thinning to normal (100 TPA) wide (60 TPA) and very wide (30 TPA) spacings and control (250-300 TPA). Underplanting of conifers (Douglas-fir, W. Hemlock, Grand fir, Sitka spruce, W. redcedar, and Pacific yew) and hardwoods (red alder and bigleaf maple) will be tested at all densities. Cost of logging, development of high and low canopy structure, growth and yield of timber, as well as micro-climatic and soil conditions will be monitored. Spacing treatments will be replicated on 4 to 6 30- to 50-acre plantations. A series of field forums bringing land managers to the experimental sites began with installation of the first replication.

NEST PREDATION IN MANAGED FORESTS: THE EFFECT OF HABITAT AND NEST LOCATION. Rav D. Entz, Eastern Washington University, Cheney, Margaret A. O'Connell, Eastern Washington University, Cheney, James G. Hallett, Washington State University, Pullman.

The decline and local extinction of avian species has been the focus of current research. Nest predation has been implicated in this decline and rates of nest predation have been shown to vary with habitat type. Riparian habitats often support greater bird species diversity and provide greater structural diversity for nesting cover. This study examined rates of nest predation in upland and riparian habitats, correlated these rates to habitat, nest location, and microhabitat conditions, and determined the predator species. Camouflaged artificial nests were placed on the ground and at 4m. Ten nests were placed at each height in both habitat types at 15 study sites in northeastern Washington. Nests were visually checked twice during three separate sampling periods between April and July, 1992. Predation was significantly higher in upland, ground-placed nests, and during the last sampling period. A strong relationship also exists between cover and nest predation.

This study was supported, in part, by the Northwest Science 1992 Student Research Grant.

BAT ACTIVITY IN MANAGED FORESTS OF THE SOUTHWESTERN CASCADE RANGE. Janet L. Erickson, University of Washington, Seattle.

To investigate the impact of land use practices on bats and other wildlife, a Timber Fish and Wildlife project entitled *Wildlife use of managed forests- a landscape perspective* was developed. As part of this project, a stand-level survey of bat communities found within three stand types of managed forests was conducted during August 1992. Patterns of habitat use were determined for clearcut, pre-commercial thin, and mature stands using ultrasonic detection. The sampling effort resulted in 1029 bat echolocation calls which were analyzed using signal processing software. Total calls were not distributed equally among sites nor among stand types. Mean detection rates were more than twice as high in clearcut and mature stands than pre-commercial thin stands. Further analysis on the basis of individual species or species group will be done to determine if shifts in species composition exist among stand types.

ROLE OF PATHOGENS IN FOREST HEALTH: RESEARCH PERSPECTIVES. Gregory M. Filip, Oregon State University, Corvallis.

Three primary disease groups play important roles in the forests of the Blue Mountains and the interior West: dwarf mistletoes, stem decays, and root diseases. Dwarf mistletoes cause growth loss and mortality especially in western larch, Douglas-fir, ponderosa pine, and lodgepole pine in northeastern Oregon. Dwarf mistletoe-infected branches provide nesting habitat for at least three species of owls, and the mistletoe plants are a preferred food source for porcupines. Stem decays cause economic loss primarily in grand fir as a result of infection chiefly from Echinodontium tinctorium and Heterobasidion annosum. Decayed grand fir trunks provide habitat for several species of birds and mammals. Root diseases are caused by several fungal pathogens; the most important are Armillaria ostoyae, Heterobasidion annosum, and Phellinus weirii in north-eastern Oregon. Root diseases cause widespread mortality in several conifer species and predispose trees to bark beetle attack. Root diseases are a major cause of canopy gaps and thus may be important in affecting forest succession and wildlife habitat.

SILVICULTURAL MANAGEMENT OF BARK BEETLE HAZARD Paul Flanagan, Forestry Sciences Lab, Wenatchee, WA

The roles of bark beetles have not changed during this century; stressed and weakened trees are still predisposed to attack. Changes in the species composition, density, and continuity of susceptible host type have occurred, often resulting in increased bark beetle populations. An understanding of fire ecology as well as beetle biology is useful in developing silvicultural prescriptions. Management guidelines are available for bark beetles, but they vary in depth of understanding.

NEST-SITE DIFFERENTIATION BY THREE SYMPATRIC CHICKADEES. Anthony Allan Floyd, Washington State University, Pullman.

To demonstrate competition-based resource partitioning it is necessary to show limitation of resources, differences in use of resources, and suppressability of resources. Nesting cavities are regarded as a limited resource in managed forests and my data show that three species of chickadees use significantly different nest sites where they are sympatric in northeastern Washington. I found significant differences for 7 of 12 nest-site variables and I used 3 of these (nest-cavity height, nest-tree type, and shading) in a discriminant function analysis. Black-capped Chickadee nests differ, significantly and predictably, from Chestnut-backed and Mountain Chickadee nests. Group separation for nests of the latter two species was less significant. These differences suggest that competition may play a role, albeit minor, in nest-site selection.

A CENTENARY SURVEY OF WASHINGTON'S FLORA.
Sarah Gage and Sharon Rodman, University
of Washington, Seattle.

In 1892 Louis F. Henderson was hired by the Washington State World's Fair Commission to make a botanical collection for exhibit at the 1893 Chicago World's Fair. This collection, housed at the University of Washington Herbarium, is a snapshot of the State's flora at the time. By consulting the specimen labels and Henderson's unpublished reports, we located as closely as we could the sites where he collected. We visited these sites in 1992, and documented and collected plants wherever possible and appropriate. A "then and now" comparison of the collection areas yields three broad categories of floristic change. In grossly disturbed sites, e.g. urban areas, we found virtually no native taxa. Areas that appeared superficially less disturbed were notable for the presence of invasive alien species not collected by Henderson. In least developed or protected areas, e.g. state parks, many of the taxa Henderson found were present in 1992. This survey can be used to create a human interest context to educate the general public about native plants, weeds, and disturbance.

MONITORING BAT USE OF OLD GROWTH
REDWOOD FORESTS: PRELIMINARY
RESULTS AND A PROPOSAL FOR FUTURE
WORK.

Steven T. Gellman, and William J. Zielinski. U.S.D.A.
Forest Service, Redwood Sciences Laboratory, Arcata,
California

Along the coast of California remaining tracts of old growth redwoods (*Sequoia sempervirens*) commonly exhibit basal hollows that provide roosting habitat for bats. Guano deposition below roost sites was monitored with the use of guano traps made from synthetic semi-permeable membranes suspended inside the hollow. These traps were checked every two weeks from 7 April to 19 August, 1992. Feces were collected, dried in an oven and weighed. 26 hollows were sampled and all were found to contain guano. Species identification was not possible using this technique though two distinct feces types regularly appeared. A mean (SD) of 1.71 (1.90) g. of guano per hollow was collected for the duration of the study, ranging from a low of 1.29 g. to a high of 10.68 g. in a two week period. Greatest concentrations occurred between 13 May and 10 June. Distance of tree hollow from Highway 101 was not correlated to guano deposition. Currently, our project has expanded its scope to look at the effects of forest fragmentation on bats use of hollows. Bat use of isolated stands will be compared to that in a contiguous forest using: 1) guano deposition in hollows, 2) ultrasound sampling, 3) mist-netting, 4) nocturnal observations using night vision equipment.

SEDIMENT DELIVERY TO HEADWATER STREAM
CHANNELS FOLLOWING TIMBER HARVEST IN THE
UPPER GRANDE RONDE RIVER, OREGON. Robert E.
Gill, USFS, Wallowa-Whitman National Forest, La
Grande, Henry A. Froehlich, Oregon State University,
Corvallis (in progress).

Many studies have focused on improving our understanding of the effects of timber harvesting activities on soil, water, and fisheries resources. Much of this work has led to the development and widespread use of soil erosion prediction models by land managers. This widespread use has often resulted in model applications that are outside the bounds in which the models were developed. There is currently no adequate method for predicting the quantity of sediment delivered to first and second order channels following road construction and harvesting in areas of ash-influenced soils of eastern Oregon. The short-term objective of this study is to validate, and potentially improve, a sediment yield prediction model for the upper Grande Ronde River watershed in northeastern Oregon. The long term objective is to use this information in the development of a sediment budget for the upper Grande Ronde River watershed. A variety of methods will be employed to accomplish these objectives. Methods include: in-channel and on-slope sediment trapping for quantity and rate determination, physical characterization of the area contributing flow and sediment, physical characterization of the soil samples themselves, and statistical analysis for extrapolation of results. This study is designed for an eight year duration in two year increments. Preliminary results will be reported in a variety of ways.

ALPINE LICHEN COMMUNITIES IN WASHINGTON
STATE. Katie Glew, University of Washington,
Seattle.

Alpine lichen communities in the Olympic National Park and the north and central Cascade Mountains are currently being studied. A preliminary annotated checklist from these regions will be presented. The checklist is a first step towards determining the species composition and ecological characteristics of lichen communities in these areas. A comparison of terrestrial and saxicolous lichens from several locations and sites will be made. Representative species include *Cetraria ericetorum*, *C. nivalis*, *C. cucullata*, *Coelocaulon aculeatum*, *Cornicularia normoerica*, *Leprocaulon albicans*, *Peltigera rufescens*, *Pseudephebe pubescens*, *Solorina crocea*, *Thamnolia subuliformis*, *T. vermicularis* and *Umbilicaria hyperborea*. Sampling was done in the Olympic National Park and the Buckhorn Wilderness Area, using a 100m transect across an elevation gradient. Slope and aspect were noted. Ten random points were selected along the transect to determine the location of lichen communities. At each of the ten points, ten 10cm² subplots were randomly selected from a 0.5m² quadrat. Percent cover of lichens was recorded.

MICROSITE EFFECT AND ANNUAL CHANGE IN SOIL MOISTURE RESPONSE TO CANOPY GAP FORMATION. Andrew N. Gray, Oregon State University, and Thomas A. Spies, USDA-FS Forest Science Lab, Corvallis.

To what extent is resource availability in forest canopy gaps modified by microsite or annual weather pattern? We studied soil moisture response to creation of different sizes of experimental gaps in old-growth and mature Douglas-fir forests in the Cascades. Microsites differed by within-gap position, substrate type, and density of understory vegetation. Relative increases in soil moisture compared to controls were similar regardless of gap size, and became greater as summer drought progressed. North edges of large gaps were drier than control areas, while south edges and gap centers remained at high water potential throughout the summer. Moisture response was affected by understory vegetation and annual precipitation patterns. We conclude that formation of forest canopy gaps is followed by increases in available soil moisture which are modified by site structure. These increases appear to be critical to plant growth and establishment.

INTESTINAL CHITOBIASE ACTIVITY IN HATCHERY AND NATURAL JUVENILE CHINOOK SALMON. Warren "J" Groberg, Oregon Dept. of Fish & Wildlife, La Grande, Becky A. Matson & Sheffie D. Surber, Eastern Oregon State College, La Grande.

The potential for hatchery-reared juvenile chinook salmon to digest chitin was evaluated using a chitobiase enzyme assay. Chitobiase activity in intestinal tract contents from chinook salmon reared in stream-water and well-water was compared to a group reared naturally in a pristine environment. Comparisons of activity were also made using a well-water group fed a diet containing erythromycin. Chitobiase activity was detected in all fish tested, regardless of their rearing environment. Using a quantal form of the assay, this activity appeared comparable between natural and hatchery-reared fish. Hatchery fish should have the ability to digest invertebrates containing chitin.

DRUMLINOIDS IN THE UPPER RIO GRANDE AREA, SAN JUAN MOUNTAINS, COLORADO. Nanci S. Grumet and Robert J. Carson. Department of Geology, Whitman College, Walla Walla WA.

Quarrying and abrasion by late Pleistocene ice in the upper Rio Grande area of the San Juan Mountains created landforms ranging from rock drumlins to glacial pavement. Because all landforms are eroded from welded tuff, lithology is not the controlling factor. Nor is ice thickness a significant factor because a variety of landform shapes and sizes exists at different elevations. Ice flow direction and azimuths of vertical joints are both factors in landform orientation, but the influence of canyon morphology is unknown. The main factor determining landform size and relief is the spacing of vertical and horizontal joints. Wide joint spacing reduces plucking and results in glacial pavement. Close joint spacing facilitates quarrying and leads to low-relief rock drumlins. It is believed that intermediate joint spacing results in high-relief rock drumlins with gentle abraded stoss sides and steep plucked lee sides.

POPULATION DENSITIES AND STRUCTURE OF ARBOREAL SPIDER COMMUNITIES IN NORTHWEST FOREST ECOSYSTEMS. Juraj Halaj, Darrell W. Ross, Oregon State University, Corvallis, Richard R. Mason, Torolf R. Torgersen, Pacific Northwest Research Station, LaGrande.

Description of spider communities is important for understanding their potential role in regulating populations of forest defoliators. Community structure and densities of arboreal spiders were estimated on lower crown branches in sapling stands of Douglas-fir (*Pseudotsuga menziesii*) in three geographical provinces; the western and eastern Coast Range and the western Cascade Range, on two dates between June and August 1992. Mean densities for the two dates were 4.6, 10.4, 5.1 and 13.0, 17.2, 9.5 spiders per square meter of branch area for the three provinces, respectively. On the second date, across all sites, web-spinning families comprised 57 % of the total spider fauna with the Linyphiidae dominating; the remainder were hunting families dominated by the Salticidae and Philodromidae. Although web-spinners were dominant overall, the Salticidae were the most abundant family in samples from the western Cascade Range representing 37 % of the total spider fauna for this province.

"NEW FORESTRY" SURVEY BY NONINDUSTRIAL PRIVATE FOREST LANDOWNERS. Donald P. Hanley, Washington State University, Paul C. Ringgold, University of Washington.

"New Forestry" is an approach to forest management that attempts to balance the production of wood fiber with other existing natural resource amenities. It developed as a result of changes in public values, as well as information regarding the effects of traditional forest management on non-timber values. The majority of new forestry demonstrations in Washington are on either public or industrial lands. Even though nonindustrial private forest (NIPF) landowners own approximately 25% of Washington's forestland, their potential use of new forestry techniques remains a largely unexplored and important arena. During a forest management field day at Pack Forest, NIPF landowners were surveyed about their opinions on two new forestry techniques: aggregated green tree retention and dispersed green tree retention. 80% of the NIPF landowners preferred either technique over a clear-cut harvest. In fact, they were willing to incur harvest costs 15% higher to implement these techniques. There was a weak correlation between acreage owned and willingness to pay increased harvest costs. Clearly new forestry techniques should be considered in planning timber harvests on NIPF lands.

PRELIMINARY OBSERVATIONS ON SEED DISPERSAL AND SEED PRODUCTION OF *CYPRIPEDIUM FASCICULATUM*. Richy J. Harrod, U.S.D.A Forest Service, Leavenworth, WA. and Richard Everett, PNW Research Station, Wenatchee, WA.

The clustered ladyslipper (*Cypripedium fasciculatum*) is listed as priority 2 by the Washington Natural Heritage Program (DNR) and appears on the U.S.F.S Regional Forester's sensitive species list. On the Wenatchee National Forest, timber sales or other projects often are planned in areas that contain clustered ladyslipper populations. Studies on the habitat requirements and reproductive biology are currently being carried out in an attempt to assist land managers in making more informed decisions concerning protection and/or management of this species. During the summer of 1992, a study was designed using seed collecting screens to determine seed dispersal. The majority of the seeds fell within 50 cm of a "cluster" of plants. Few seeds were recovered on collection screens as compared to the numbers produced; a mean of 4151 per fruit. A significant increase in peduncle length occurred during fruit maturation. Height of peduncle at full fruit was significantly correlated with numbers of fruits produced per aerial stem. Numbers of fruit per stem varied from 0 to 3. These preliminary results suggest that clustered ladyslipper may be limited in distribution because of poor dissemination. Future studies are being planned and will be presented.

DOES INCREASING CO₂ REALLY CAUSE GLOBAL WARMING? Jan A. Henderson, USDA Forest Service, Mountlake Terrace WA.

The implications of the effects of atmospheric pollution on the global environment and global economics is one of today's major problems. It has been the subject of considerable scientific and political debate for many years and is one of today's most published subjects. The "greenhouse" effect of atmospheric CO₂ on earth's climate has become a subject of everyday conversation and is popularly referred to as "global warming." Atmospheric CO₂ has risen from about 280 ppm earlier in the century to about 355 ppm today and is commonly predicted to rise to 400 to 700 ppm in the foreseeable future. Global temperatures are predicted to rise 2-5 °C under this scenario. This phenomenon was regarded as an hypothesis and subjected to an empirical test. The long-term CO₂ and temperature relationships from antarctic ice cores and modern northern hemisphere temperature relationships for the period of the modern CO₂ increase were examined to see to what degree the empirical evidence could support the hypothesis. No positive correlation was found in the modern temperature records that supports the hypothesis that rising CO₂ causes global temperatures to rise. The ice core data suggest a strong correlation between temperature and CO₂, but the appropriate interpretation appears to be that rising temperatures cause atmospheric CO₂ levels to rise.

LINKING BAT ACTIVITY WITH LANDSCAPE-LEVEL ATTRIBUTES USING GIS. Mark H. Huff, John F. Lehmkuhl, and John A. Young, USDA Forest Service, Pacific Northwest Research Station, Olympia, WA.

Bats studied in Douglas-fir forest stands of the Oregon Coast Range were substantially more active in older stands than younger ones. Their activity patterns in these forests were confined mostly to dusk and dawn, suggesting that these stands were used for roosting and the bats foraged elsewhere in the landscape. Our objective was to examine the association between landscape characteristics and stand-level bat activity. Three landscape sizes, circular bands of 500, 1500, and 2500 m (radii) from the center of bat survey stands, were classified by physical and vegetative features. Age class of stands surveyed for bats was the best indicator of bat activity; landscape features were generally poor indicators.

IS THE BARRED OWL REPLACING THE SPOTTED OWL IN WESTERN WASHINGTON? Wayne Iverson, Biology Department, Western Washington University, Bellingham, WA 98225.

The interaction of two congeneric owls (genus *Strix*) is being analyzed based on population census and home range data from the West Slope of the Washington Cascades. The barred owl (*S. varia*) is an exotic species which entered Western Washington within the last 30 years. Its nesting and foraging habits overlap with those of the northern spotted owl (*S. occidentalis caurina*), a subspecies protected by the Endangered Species Act. Competition with the barred owl is therefore a concern for a successful spotted owl conservation strategy. Species association is being evaluated, along with behavioral interactions. Where barred owls are shown to be displacing spotted owls, site characteristics will be defined.

Renovating the Vegetation Mosaic of the Blue Mountains: Restoration of Ecosystem Components and Processes

Charles G. Johnson, Jr., Area Ecologist, Malheur, Umatilla, and Wallowa-Whitman National Forests, Baker City, OR

Biological diversity can be enhanced by changing our management strategies. Managing at the landscape level will provide greater health, more vigorous plant response, and an overall improved vitality of component species. Reintroduction of fire, retention of important stand segments, restoration of plant communities, and promotion of certain species are fundamental actions needed to restore health and enhance biological diversity in the Blue Mountains. With our land stewardship over the past century, fire has essentially been removed as a fundamentally important component of the forest and grassland ecosystems. Participation by fire in the ecological life cycle of the vegetation requires that it be ongoing at appropriate intervals and intensities. By emphasizing landscape level planning and project implementation in the Blue Mountains, the current harvest of coniferous tree species by defoliators should diminish over time.

MANAGEMENT AND MONITORING OF FOREST DISEASES. Alan Kanaskie, Oregon Department of Forestry, Salem.

Throughout most of the twentieth century, diseases have been known primarily for destroying an enormous volume of wood in forests of the interior Pacific Northwest. Losses continue at high levels due in part to past silvicultural practices, which have increased the severity of root diseases, dwarf mistletoes, and stem decays in many areas. However, properly conceived and applied silvicultural manipulations can reduce impacts of diseases on management objectives. Contemporary forest managers now recognize that forest pathogens play various roles in the ecosystem, creating gaps, influencing biodiversity, and providing habitat for certain forest inhabitants. Intelligent management depends heavily on reliable disease detection through forest inventories or special surveys. Information can be incorporated into management plans using various disease and forest growth models.

FOREST HEALTH IN OREGON AND IDAHO: ECOLOGICAL SIMILARITIES, POLICY DISPARITIES. James G. MacCracken and Jay O'Laughlin, University of Idaho, Moscow.

Forest health issues have become important in both southern Idaho and northeastern Oregon. The Wallowa-Whitman (WWNF) and Boise (BNF) National Forests provide examples. Both forests are within Bailey's Rocky Mountain Forest Ecoregion, have endured a 6-year drought, have a similar forest management history, and have a recent epidemic of defoliating insects with significant tree mortality. The problem has been at the forefront longer with the WWNF than the BNF. Both forests have adopted forest health strategies that differ in many ways. Each forest defines forest health differently. Salvage logging is a major feature of both strategies, but the BNF has declared an emergency and exempted salvage sales from the appeals process. The WWNF places greater emphasis on the role of fire in future management, and takes a more holistic approach to forest health.

HABITAT QUALITY AND ACTIVITY BUDGETS OF MOOSE IN ALASKA. James G. MacCracken, University of Idaho, Moscow, Victor Van Ballenberghe, USFS, PNWRS, Anchorage, AK.

Large ruminants spend most of their time acquiring and processing forage. Forage abundance and digestibility are probably the most important components of habitat quality for moose (*Alces alces*) in many areas. We examined the hypothesis that activity budgets are related to habitat quality with data from the Copper River Delta, Denali National Park, and the Kenai Peninsula, Alaska. The length of foraging bouts was weakly related ($P > 0.05$) to forage abundance ($r^2 = 0.13$) and diet digestibility ($r^2 = 0.11$). However, ruminating bout length was strongly ($P < 0.05$) related to both forage abundance and diet quality ($r^2 = 0.72$ and 0.97 , respectively). Foraging bouts are a function of forage abundance and selective behavior, and are highly variable. Ruminating bouts are constrained primarily by diet digestibility and are a good predictor of forage-based habitat quality.

FOREST PEST RELATIONSHIPS TO SPOTTED OWL NESTING HABITAT, EASTERN CASCADE RANGE, WASHINGTON. Sandra K. Martin, Jerome S. Beatty, and Frank Hawksworth, USDA Forest Service, Wenatchee WA, Portland OR, and Ft. Collins CO.

Northern spotted owls (*Strix occidentalis caurina*) do not construct their own nesting structures, but they have been known to use cavities in snags and in live trees, and dwarf mistletoe brooms. More than half of known nests in the eastern Cascade range in Washington have been found in dwarf mistletoe brooms. We characterized spotted owl nests in dwarf mistletoe brooms and characterized nesting habitat, including forest insect and diseases parameters. Spotted owls selected significantly more large dwarf mistletoe brooms as nests than statistically expected. Forest stands containing dwarf mistletoe nests had significantly smaller trees and snags, significantly higher dwarf mistletoe infection levels, and were further from the Cascade crest than forest stands containing cavity nests. Other site and stand attributes were similar between these nest stand types. Dwarf mistletoe infection should be carefully considered as one component of the eastside forests that could be actively managed when the goal is to maintain, or to create, spotted owl nesting habitat.

TEMPERATURE AMELIORATION UNDER MIXED CONIFER SHELTERWOODS ON FROST PRONE SITES IN THE SOUTHERN OREGON CASCADES. L.A. McCrimmon and W.H. Emmingham, USDA Forest Service, Siskiyou National Forest, Grants Pass, Oregon. Oregon State University, Corvallis.

Frost during the growing season has been documented over large areas of the southern Oregon Cascades. Six sites were studied on the Rogue River National Forest in 1989 and 1990 to determine the effects of varying canopy density on the severity, frequency, and duration of frost events. At each site stands of varying canopy densities were compared with clearcuts or openings. Canopy density was measured by basal area per acre, percent crown cover, and Kingsley's points. Average half hourly temperatures were collected at 8 inches and 42 inches above the ground. Increasing canopy density significantly decreased severity, frequency, and duration of frost events. Regression equations relating canopy density to severity, frequency, and duration were developed. This study was funded by the Rogue River National Forest.

EPIPHYTE BIOMASS ESTIMATED FROM LITTER IN *PSEUDOTSUGA-TSUGA* FORESTS. Bruce McCune, Oregon State University, Corvallis.

How well can litter be used to estimate epiphyte biomass? To answer this, the standing crops of epiphyte litter and epiphyte biomass were estimated independently in each of three *Pseudotsuga-Tsuga heterophylla* stands in the Cascade Range. Litter was collected in late summers of two years in 20, 2-m radius plots. Groups of trees were felled and sampled for epiphytes. Samples were sorted into four groups: cyanolichens, alectoroid lichens, other lichens, and bryophytes. For lichens, biomass of litter (L) was strongly related to epiphyte biomass (B) ($r^2=0.87$, $n=18$), in about a 100:1 ratio ($\text{sqrt}(L)=0.1*\text{sqrt}(B)$). Year-to-year variation was smaller than the differences among stands. Ten plots are recommended for stands with simple structure and 15 plots for older stands with more complex structure. The method is not recommended for bryophytes because bryophyte litterfall is highly aggregated. The method is recommended for large-scale surveys of lichens and other studies where large differences in epiphyte biomass are expected.

HISTORICAL CHANGES IN ANADROMOUS FISH HABITAT IN THE UPPER GRANDE RONDE BASIN. Bruce A. McIntosh and Sharon E. Clarke, Oregon State University, Corvallis, James R. Sedell, Pacific Northwest Research Station, Corvallis.

The U.S. Bureau of Fisheries conducted stream surveys in the Upper Grande Ronde Basin in 1941. This survey was part of an extensive inventory of stream habitat conditions for anadromous salmonids (*Oncorhynchus* spp.) throughout the Columbia River Basin. The survey systematically inventoried 165 km of streams within the 3000 km² watershed. Habitat was degraded from land-use activities (timber harvest, road construction, stream channelization, livestock grazing, and mining) and natural events (drought, flood, and fire) prior to the 1941 survey. A 1990 resurvey determined how stream habitat conditions had continued to change. The historical survey and the 1990 resurvey inventoried streams according to pool and bottom substrate characteristics. Losses in large pools (> 1-m depth and > 20-m² area) ranged from 28-86% throughout the basin, while substrate composition has shifted toward smaller size-classes, with significant increases in fine sediment. In an era of presumably improved management (1941-1990), large-scale losses continued to occur in both the quantity and quality of habitat necessary to the continued viability of resident and anadromous fish populations.

EFFECTS OF PARTIAL BARK-REMOVAL ON THE GROWTH OF PACIFIC YEW. Don Minore, Pacific Northwest Research Station, Corvallis, OR.

Harvesting only a portion of the bark on standing yews (*Taxus brevifolia* Nutt.) would provide bark for taxol production with minimal effects on stand structure if the affected trees continued to grow, but it would be expensive and wasteful if those trees died. A retrospective approach was used to determine growth for periods of 3 to 92 years after the partial bark-removal caused by windthrow or logging damage in 121 scarred yew trees. Radial growth of the scarred trees did not differ from the growth of nearby unscarred yews. Radial growth after scarring was strongly correlated with growth before scarring and only slightly correlated with overstory canopy density, elevation, and the amount of bark removed. Partial bark-removal probably will not seriously affect the growth of Pacific yew if less than 50% of the bark is removed.

BRYOGEOGRAPHY OF THE HUMID PACIFIC NORTHWEST

D. H. Norris, Oregon State U

In comparison with such areas as the S. Appalachians or maritime western Europe, the bryophyte species diversity in the humid NW is surprisingly low. Such low species diversity is to be expected because of the peninsular nature of the Pacific Northwest humid regions. In response to climatic pulses, a peninsular geography allows only a north-south shifting of the members of a single flora. In contrast, repeated climatic pulses in a non-peninsular flora continuously enrich the flora by inputs from all neighboring areas.

ALL AGE, MULTIPLE SPECIES FOREST MANAGEMENT. W.H. Oberteuffer, Smilin' O Ranch, Elgin, OR

The use of an all age, multiple species forest management system will greatly benefit forest health; help stabilize forest dependent communities; increase natural salmon production; improve soil conditions; be more supportive of natural vertebrate and invertebrate populations; improve entire watersheds, including riparian areas; produce more wood fiber, grass, fish and game and water for man's ultimate use.

COMPUTER AIDED PLANT IDENTIFICATION. Richard R. Old, XID Services, Inc., Pullman, Washington.

Recent technological developments have opened the door to some exciting opportunities in the field of plant identification. Rather than attempting to answer a rigid series of questions in a standard dichotomous key, the user can now access the data in a manner consistent with their skill level and plant specimen. From a menu-driven computer program, the user selects any character of their choice, i.e., flower color, milky juice, leaf length, etc. The program then eliminates from the database all species that do not match the selected character, i.e., Canada thistle is eliminated when "flower color = yellow" is selected. The user then selects another characteristic and continues to reduce the database. If, at any point, the user is unsure of what character to select, the computer can be queried as to the best selection to make. The user is then presented with a list of suggestions in order of their relative effectiveness in reducing the database. This approach can be used for all or part of the identification process. Help is available at all stages of the program. A complete authoring system is available which means that the characters, character states, help screens, references, and text screens can be completely customized to identify any group of objects or species.

VEGETATION AND SOIL PATTERNS IN THE IMNAHA RIVER DRAINAGE. Robert J. Ottersberg and Berta A. Youtie, LaGrande, Oregon.

Soil morphology was described and species frequency data was collected at two sites showing the mosaic pattern of perennial bunchgrass stands intermixed with patches of annual grasses and forbs. The bluebunch wheatgrass (Agropyron spicatum) community is associated with the moderately deep Innaha soil series at Site 1. At the same site the deep Clearlake soil series is associated with a dominance of annual bromes and mustards such as cheatgrass (Bromus tectorum) and jim hill tumblemustard (Sisymbrium altissimum). At Site 2, the moderately deep Mallory soil series is associated with annuals while the shallow Gwinly soil has perennials. Analysis of soil laboratory tests indicate that soil depth and water holding capacity have a stronger correlation to plant community than do chemical factors of soil fertility. Indicators of gopher activity have a strong positive correlation to annual species frequency and may explain species composition better than soil.

DEFOLIATORS: MANAGEMENT AND MONITORING. David L. Overhulser Oregon Department of Forestry, Salem.

Periodic outbreaks of two tree defoliators, the western spruce budworm and Douglas-fir tussock moth, have a significant influence on forest management in the interior Pacific Northwest. Monitoring systems are available that identify stands where defoliator populations may cause serious damage. Forest managers utilize this information in applying long-term and short-term approaches to reducing the impacts of defoliation. The long-term approach, silvicultural treatment, strives to create stands that are less susceptible to damage in future outbreaks. Suppression of defoliator populations using insecticides, a short-term approach, can protect valuable stands for several years. Both population suppression programs and silvicultural treatments have controversial elements.

THE DISTRIBUTION AND ABUNDANCE OF AMPHIBIANS AND REPTILES (ESPECIALLY OBLIGATE AQUATIC/RIPARIAN) ALONG THE TRUCKEE RIVER. Howard R. Panik, Western Nevada Community College, Carson City, Sherry Barrett, U.S. Fish and Wildlife Service, Reno.

Thirty-one study sites distributed along the entire length of the Truckee River were censused three times during the summer of 1992. Amphibian larvae were collected and identified by examining the mouth parts with a stereomicroscope. Ambient and water temperatures, water pH, rate of flow, and water depth were recorded at the study sites. Of the total number of 12 amphibian and reptilian species observed, five species (42%) were obligate aquatic/riparian species: Western Toad (Bufo boreas), Pacific Treefrog or Pacific Chorus Frog (Hyla regilla or Pseudacris regilla), Northern Leopard Frog (Rana pipiens), Bullfrog (Rana catesbeiana) and Western Aquatic Garter Snake (Thamnophis couchii). Of these five, only the Northern Leopard Frog was rare, and only a low number was observed at only one of the 31 study sites. Also, no larvae of this species were observed. It appears that the Bullfrog is having a negative impact on this species in the Truckee River. The distribution pattern of the four amphibian and the eight reptilian species varied considerably. Only two of the 12 species had a distribution along the entire 100 mile stretch of the river: Pacific Treefrog or Pacific Chorus Frog and Western Terrestrial Garter Snake (T. elegans).

INTERRELATIONSHIPS OF WATER-STRESSED GRAND FIR, WESTERN SPRUCE BUDWORM, AND ARMILLARIA ROOT DISEASE. Catherine A. Parks, Forestry and Range Sciences Laboratory La Grande, Gregory M. Filip, Oregon State University, Corvallis.

Drought-stress affects nutritional quality, digestibility and chemical defenses in foliage and roots of host trees. Western spruce budworm (Choristornuera occidentalis) fed on water-stressed grand fir (Abies grandis) seedlings had higher survival rates and grew faster and larger than budworm fed on well-watered seedlings. Infection and mortality rates of seedlings inoculated with Armillaria ostoyae were higher in water-stressed treatments, unless seedlings were also defoliated by budworm. Total phenols and soluble sugars were higher in roots of undefoliated, water-stressed seedlings. Short-term defoliation by budworm enhanced survival of water-stressed trees by reducing transpiration loss and utilization of reserve carbohydrates (starch).

A SURVEY OF CONIFEROUS FOREST MOSSES ALONG AN ALTITUDINAL AND SUBSTRATE GRADIENT. Jeri Lynn E. Peck, Oregon State University, Corvallis.

As the harvest of moss as a secondary forest product has risen, an understanding of the distribution of mosses has become more important in management considerations. During the summer of 1991, thirteen stands at the H.J. Andrews Experimental Forest and two in the Wildcat Mountain Research Natural Area in the western central Cascades were examined for species richness and coverage along an altitudinal gradient on the forest floor, logs, and tree bases. Species richness and coverage decrease with increasing altitude and decreasing temperature. Snow creep at high elevations may be a significant factor affecting moss coverage on the forest floor and logs. Cluster analysis indicates that moss species have substrate preferences and that these preferences remain constant along an altitudinal gradient. Moss associations vary along a temperature and moisture gradient with the impact of snow creep and with the response of individual species to the gradient. Future investigations may elucidate guidelines for harvest management.

IMPLICATION AND BENEFITS OF LONG TERM BAT MONITORING IN NATIONAL FORESTS. J. MARK PERKINS, WILDLIFE CONSULTANT.

Knowledge of forest bat species which are the primary predators of adult insect forest pests, is scant at best. Here I present rationale for long term monitoring, and surveys and implications of results. Benefits of such monitoring include providing accurate and locally significant data for fulfillment of governmental regulations concerning preparation of BE's, EA's, EIS's and mitigation plans. Recent monitoring indicates past and present silvicultural practices do militate against these valuable predators. Surveys which span 15 yrs and four forests indicate harvest of most large trees heavily impacts the smallest bat species, but all bat species are negatively affected. Additional studies are suggested to clarify forestry practices impacts, set minimum survey standards and determine status of species whose population dynamics and distribution are poorly defined.

CHANGING THE LOOK OF HIGH SCHOOL BIOLOGY: CAN STUDENTS DO BATS?

Author: Stuart Perlmeier, York Univ.
Presenters: Pat Greenlee, Aimee Hart,
Jesse Fittipaldi, Willamette N.F.
and Springfield H.S

Through a challenge cost-share agreement with the U.S.F.S., students assisted in a preliminary census of bat populations for the Willamette N.F. This project provided the Forest Service with baseline data on the types and numbers of bats found at select sites. The second phase will investigate day roosting patterns of several species to determine if roost site selection is dependent on Pacific N.W. old-growth. Understanding bat roost selection will enable forest officials to make more informed management decisions. This project succeeded in training students in the methods of sampling bats. Many night roosting sites were found. It also resulted in the location of a large Plecotus townsendii maternity roost that is now protected. Carrying out this research with students gives them a window into the world of field research, provides a pool of eager and competent researchers at a reduced cost to the F.S. and provides students with the opportunity to educate others about the role of bats in the ecosystem.

LONGTERM DROUGHT RESPONSE IN SCABLAND WETLANDS OF EASTERN WASHINGTON 1986-1992. Robert R. Quinn. Eastern Washington University, Cheney.

Deficits of 20-30% in winter precipitation from 1986 through 1992 have resulted in the loss of hydrologically functioning wetlands in over 80% of the permanent shallow lakes and ponds in Eastern Washington. Ecological impacts have been severe with wet meadow vegetation types now dominating in areas previously occupied by submerged aquatic bed vegetation. In Turnbull Wildlife Refuge, 1992 air photos reveal 90% of the seasonal and permanent wetlands were dry in June 1992.

CARDIOVASCULAR ADJUSTMENTS OF THE GARTER SNAKE DUE TO TEMPERATURE VARIATIONS. Frances R. Ragsdale and Andrew T. Gannon, University of Nevada, Las Vegas.

Reptiles use a suite of behavioral and physiological mechanisms to cope with environmental temperature fluctuations. Cardiovascular adjustments must accompany changes in temperature to meet the metabolic demands of the snake's tissues. Therefore, the objective of this study was to determine baseline information for the garter snake, *Thamnophis radix*. The design of the snake body allows for the placement of a single electromagnetic flowcuff around the arterial outflow of the heart. Like all reptiles previously examined, garter snakes demonstrate increased cardiac output and heart rate with increasing temperature. Stroke volume decreases with increasing temperature, but this may reflect a decrease in filling time for the heart during each beat. These data are similar to the findings for other snake species.

FOREST CANOPY LICHENS OF CENTRAL IDAHO. Roger Rosentreter, Bureau of Land Management, Boise, Idaho.

The composition and biomass of forest canopy lichens in central Idaho was quantified by several methods. Cover class values were assigned, litter-fall was collected, and the longest length of the pendant lichens were measured. These measurements were repeated at 450 sites by habitat and cover type. Forest cover types included lodgepole pine, Engelmann spruce, Douglas fir, larch, subalpine fir, and grand fir. *Bryoria fremontii*, *B. fuscescens*, and *B. pseudofuscescens* were the dominant lichens in all forest habitat types of central Idaho. *Bryoria fremontii* was most frequent in the dry Douglas fir habitat type. Lichen biomass calculated from litter-fall had a mean of 0.112 g/m². This represents much of the annual litter-fall produced each year. Actual canopy biomass would be much greater. The alectoroid growth form was by far the most common in Idaho forests. Preliminary data suggests that the longest lichen measurement did not correlate with cover class values or biomass. Canopy cover class values serve as rapid estimates of lichen biomass.

WESTERN BARK BEETLE RESEARCH - PAST, PRESENT, AND FUTURE. Darrell W. Ross, Oregon State University, Corvallis

Several species of bark beetles in the family Scolytidae are of major ecological and economic importance in western coniferous forests. Early efforts to prevent bark beetle damage in managed forests involved direct controls. With the development of hazard and risk rating models emphasis shifted to the prevention of beetle-caused losses through silvicultural treatments. These models have evolved from simple visual guides to computer expert systems such as one recently developed for the spruce beetle in southeast Alaska. The identification of bark beetle pheromone systems provided another valuable tool for managing populations. For the past two years, there has been a federally funded initiative to develop pheromone-based strategies for bark beetle management. Future research challenges will include improving our understanding of bark beetle biology and ecology, developing new and improved hazard and risk rating models, and developing approaches for managing bark beetles in the context of ecosystem management.

SURVEY PROTOCOL AND AN INTERIM SPECIES CONSERVATION STRATEGY FOR *PLECOTUS TOWNSENDII*. Tim Schommer, Wallawa-Whitman National Forest, Baker City, Mark Perkins, Portland State University, Portland.

A survey protocol and interim species conservation strategy for Townsend's big-eared bat was developed for biologists who are involved in field surveys and bat conservation in the Blue Mountains. A natural history review summarizes our current knowledge of *P. townsendii* biology. Known distribution in Washington and Oregon indicate about 1,570 individuals, most of which are concentrated in 5 areas. Survey techniques and equipment were recommended for both winter and summer habitat. Three different levels of survey expertise were identified, and recommendations for a certification policy were reviewed. Detailed management guidelines, designed to protect and conserve this species and their habitats, are recommended for: mining operations, pesticide use, timber harvest, bridge and road construction, and human disturbance.

PSEUDO-ROCK GLACIER, TAMARACK MOUNTAIN, NORTHEASTERN OREGON. Jessie O. Schroeder and Robert J. Carson, Department of Geology, Whitman College, Walla Walla, WA.

An incipient lobate-shaped rock glacier on the southeast flank of Tamarack Mountain in the northeastern Elkhorn Mountains was reported by Barrash *et al.* (1980). The 0.1 km² field of angular blocks ranges in elevation from 1350 m to 1500 m. The large lower block field is joined to the upper block field (with bedrock outcrops) by a talus. The talus is partly tree-covered and stable, but contains small active solifluction lobes with slopes as steep as 46°. Beneath the andesite flow which is the source for the blocks must be fines (tuff and/or soil) to provide the matrix for solifluction. Indeed, the subtle ridges on the lower block field (which has a mean slope of 6°) suggest flow in the past. However, the lower block field does not have the thickness or the steep front indicating that it was ever a rock glacier. Furthermore, the field of blocks is far below the 2075 m paleosnowline indicated by cirque floor elevations and accumulation-area ratios for Pleistocene glaciers in the Elkhorns. This periglacial feature is best classified as a block slope (White, 1976). Lichenometry indicates that the feature is more than 700 years old.

PRELIMINARY OBSERVATIONS ON MACROFUNGI IN OLD GROWTH SITKA SPRUCE FORESTS. M. T. Seidl, G. Walker & J. Ammirati, Department of Botany KB-15, University of Washington, Seattle, WA 98195.

Fungi were inventoried for one season to gather baseline data for a long-term study of fungal diversity in old growth conifer forests of the Pacific Northwest. Specimens were collected from the Quinault Research Natural Area, Grays Harbor County, Washington, an old growth spruce-hemlock study area. An overview of fungus species richness and patterns of phenology will be presented. Various sampling techniques were utilized to determine feasibility. Future plans and directions of this research will be discussed.

A COMPARISON OF THE MICROHABITAT USE BY BULL TROUT, *SALVELINUS CONFLUENTUS*, IN FOUR EASTERN CASCADE STREAMS, WASHINGTON. Hilda Sexauer, Central Washington University, Paul W. James, Central Washington University, Ellensburg.

A study was initiated in July 1992 to determine habitat use by bull trout, *Salvelinus confluentus*, in four streams in the Yakima and Wenatchee River drainages in central Washington. The objectives of this study were to determine the rearing density of juveniles and the habitat use by juveniles and prespawning adult bull trout. Bull trout microhabitat and population estimates were completed by night-snorkeling techniques. The variables measured at each fish site were depth, velocity, and substrate. The juveniles were usually found in the shallow channel margins with a mean depth and velocity of 28 cm and .0003 m/sec. The prespawning adults were found in areas with a mean depth of 45 cm and a velocity of .07 m/sec. The substrate use by the fish appear similar. This data on the juveniles and prespawning adult bull trout suggest a slight variation in habitat use.

GERMINATION, RADICLE ELONGATION, AND ROOT GROWTH OF TWO ANNUAL GRASSES, TWO FORAGE SPECIES, AND YELLOW STAR-THISTLE. Roger L. Sheley, Larry L. Larson, D.E. Johnson, Oregon State University, Corvallis.

Introduced winter annuals are becoming a major component of the vegetation on foothill rangelands of southwestern Oregon. Rapid germination and root growth have been identified as important plant characteristics in arid environments. This study evaluates germination, radicle elongation and root growth rates of two annual grasses, two forage species, and yellow starthistle (*Centaurea solstitialis*). We monitored germinating seeds of each species in petri dishes on 12 h intervals for 144 h. Radicle elongation was measured on simultaneously germinated seeds on 24 h intervals for 96 h. Lateral and geotropic root growth was measured on glass-faced boxes at 4 d intervals beginning on day 2 and ending on day 18. Yellow starthistle germination, radicle elongation and root growth was faster than that of medusahead (*Claiatherum caput-medusa*) and hedgehog dogtailgrass (*Cynosurus echinatus*). Subterranean clover (*Trifolium subterraneum* var. Mt. Barker) possessed rapid seedling growth characteristics similar to yellow starthistle, whereas Palestine orchardgrass (*Dactylis glomerata* var. Palestine) was most delayed.

THE DISTRIBUTION OF SELECTED MEIOBENTHIC MICROINVERTEBRATES IN NORTHEASTERN OREGON STREAMS. Dennis Swanger, Eastern Oregon State College, La Grande.

The relationships between environmental structure and species distributions are at the core of all interesting biogeographic patterns. Periodically during the summer of 1992, benthic samples from eighteen streams (29 locations) were collected and returned to the lab for microinvertebrate identification. Thirty-one different microinvertebrates, including various ciliate genera, rotifers, gastrotrichs, nematodes, annelids, tardigrades, cladocerans, copepods, and microscopic aquatic insect larvae, were quantified in these samples. Comparisons were made utilizing a percentage similarity matrix between paired streams. Of the sampled streams, low similarity (less than 10%) was found in nine percent, high similarity (more than 80%) occurred in two percent, and eighty-nine percent were intermediate in their similarity. The six sites with the highest levels of similarity were widely separated and exhibited apparent large-scale habitat differences. Further studies incorporating the microhabitats in these streams, the effects of the drought last summer, and the sensitivity of the similarity matrix need to be made.

TREE IMPROVEMENT PROGRAM IN THE LANGXIANG FORESTRY BUREAU, CHINA. Oscar Sziklai, University of British Columbia, Vancouver, Zhang Fengchun, Langxiang Forestry Bureau, China.

The project began in 1984 as part of the technical cooperation between CANADA-CIDA (Canadian International Development Agency) and the People's Republic of China to implement integrated intensive management in the Langxiang Forestry Bureau, Heilongjiang Province. The Tree Improvement program was developed for the three most important species - *Pinus koraiensis*, *Picea koraiensis* and *Larix gmelini*, which provide 83% of the close to 15 million seedlings planted yearly on approximately 5,000 ha. Applying the conventional phenotypic selection, close to 500 plus trees were selected, scions and cones were collected. A 10 ha. clonal and seedling seed orchard was established. For the required number ramets crown-cleft graft was used, while open pollinated 2+0 seedlings were planted in the seedling seed orchard. Six ramets from each plus trees are preserved in a 3 ha. clone bank, and any new selection will be included in the clone bank to maintain a wide genetic base for the future development.

SEDIMENTATION CHARACTERISTICS OF *Giardia lamblia* CYSTS AND THEIR RELEVANCE TO STANDARD METHODS FOR DETECTION OF *Giardia* IN WATER. David J. Thomas, Central Washington University, Ellensburg.

Giardia is the most commonly identified cause of waterborne gastrointestinal disease in the United States. Reliable methods of detecting *Giardia* cysts in water are still in experimental stages. The current standard method for detecting *Giardia* cysts calls for an overnight period of sedimentation to concentrate the cysts. This protocol, while not directly citing any particular research, appears to be based on, or at least supported by research performed on *G. muris* (a species which is not pathogenic to humans). This research determined that *G. muris* has a sedimentation rate of 1 cm/hr in Percoll. No published research has been performed to confirm that purified *G. lamblia* cysts in water behave in the same manner. I am currently investigating this problem using aged and fresh *G. lamblia* cysts. Results obtained so far indicate that *G. lamblia* cysts have a sedimentation rate much lower than 1 cm/hr. Based on these findings, I recommend that the sedimentation time be increased to 48 hours, or eliminated in favor of centrifugation.

INFLUENCE OF WESTERN JUNIPER DEVELOPMENT ON SOIL NUTRIENT AVAILABILITY. Arthur R. Tiedemann, Pacific Northwest Research Station, LaGrande, OR, James O. Klemmedson, University of Arizona, Tucson.

In 1988, we initiated studies to assess the influence of western juniper (*Juniperus occidentalis* Hook.) invasion and development on nutrient accumulation patterns in sagebrush/grass ecosystems of central Oregon. The objective of this part of the study was to assess nutrient availability changes in the soil as juniper invaded and advanced to maturity. Bioassay in a growth chamber with barley as a test plant was used to determine nutrient availability. We collected the surface 15 cm of soil from beneath juniper canopies (canopy soil) and intercanopy areas (intercanopy soil) for 5 age classes of trees ranging from 36 to 160 yr. Nutrient availability in these soils was compared to an area with little or no juniper invasion (open soil). Compared to open soils, P availability of intercanopy soils was significantly reduced for the two oldest tree classes. In canopy soils, advancing juniper maturity caused first an increase in P availability and then a decline with the oldest tree class. The most striking effect of juniper was an increase in S availability in canopy soils with advancing juniper maturity.

VESICULAR-ARBUSCULAR MYCORRHIZAE AND PRIMARY SUCCESSION ON MOUNT ST. HELENS. Jon H. Titus and Roger del Moral, University of Washington, Seattle.

Twelve years after the eruption of Mount St. Helens, primary succession is still in its early stages. The distribution of vesicular-arbuscular mycorrhizae (VAM) and VAM propagules was assessed on the Pumice Plains. Mycorrhizal plants and propagules were absent from rills, exposed pumice, and near rocks, but occurred near mounds resulting from lupine growth and in recovering vegetation. The seeds of seven major pioneer species were planted in constructed microsites, half of which had been inoculated with VAM. Plant growth parameters are being monitored to determine how microsites and the presence or absence of VAM propagules affects these pioneers. All species show significantly greater growth in lupine mounds. *Anaphalis margaritacea* showed a negative growth response to VAM propagules and *Carex mertensiana* showed a positive response. Other pioneer species appeared indifferent to the presence of VAM propagules. These preliminary results suggest that mycorrhizae play a minor role in early pioneer succession on Mount St. Helens.

CHARACTERISTICS OF LOGS UTILIZED BY ANTS IN PILEATED WOODPECKER HOME RANGES IN NORTHEASTERN OREGON. Torolf R. Torgersen and Evelyn L. Bull, Forestry and Range Sciences Laboratory, La Grande.

Log-inhabiting ants are a major prey item for pileated woodpecker (*Dryocopus pileatus*) in northeastern Oregon. Species of *Camponotus* and *Formica* are the most common ant taxa in woodpecker diets. These same taxa were dominant among the ants found in logs in the pileated woodpecker home ranges studied. Thirteen species of ants were represented in collections obtained by cutting subsamples of logs into 1-m-long bolts on 20 X 20-meter plots. There were 240 such plots in 12 woodpecker home ranges. *Formica*, represented by six species, numerically dominated the collections - accounting for about 20% of all the ants found. Three species of *Camponotus* comprised 12.5% of the collections. One species each of *Lasius*, *Tapinoma*, *Leptothorax*, and *Aphaenogaster* comprised the remainder of the ants found. The log census indicated a density of 289 logs per ha. About 17% of the logs were in the larger size-classes (38-120cm). *Camponotus* species were most commonly found in these large-diameter logs. Neither *Formica* nor the other species of ants showed preferences for log-size. Most taxa of ants tended to be found in moderately decayed wood, except for *Camponotus* which favored sound logs. Logs of each tree species - firs, pines, and larch - had different ant taxa associated with them. Size-class distribution and density of logs have implications for ecological forest management. Down logs are foraging habitat for pileated woodpeckers. Woodpecker nest cavities provide nesting sites for secondary cavity-nesters that are important predators of the western spruce budworm and the Douglas-fir tussock moth. All but one of the nine species of *Camponotus* and *Formica* found in the down logs are also documented predators of budworm or tussock moth.

SIMULATED STAND DYNAMICS OF YOUNG DOUGLAS-FIR PLANTATIONS THINNED TO ENHANCE STRUCTURAL DIVERSITY. Gabriel F. Tucker, COPE Program, Oregon State University, Stuart R. Johnston, Siuslaw National Forest, William H. Emmingham, Forest Science Department, Oregon State University, Kathleen G. Maas, COPE Program, Oregon State University

The ORGANON growth analysis projection model (Western Willamette Valley Version) was used to simulate different levels of commercial thinning in 30-year old pre-commercially thinned Douglas-fir plantations. Data was collected from one acre permanent plots located near Mapleton, Oregon, at the first of several sites of this interdisciplinary ecosystem management project. Overstory treatments included thinning to 30, 60, and 100 trees per acre (tpa) plus an uncut control (approx. 225 tpa). Model output included variation in average tree dbh, total tree height, canopy closure, crown length, and stand density over time. Results show differences for each of these parameters. The stand modeling provides an estimate of the impact that such treatments have on stand structural diversity important to many coastal forest organisms. The long-term results of the project will, in turn, be used in future modelling efforts to simulate stands of increased structural complexity.

A COMPARISON OF THE FOOD HABITS OF WILD RAINBOW TROUT AND HATCHERY-REARED STEELHEAD TROUT IN THE YAKIMA RIVER BASIN. M. Scott Urakawa, Central Washington University, Ellensburg, Paul W. James, Central Washington University, Ellensburg.

A study was initiated in the spring of 1991 to determine the food habits of introduced hatchery-reared steelhead and wild rainbow trout in a tributary of the Yakima River. The objective of this study was to determine how hatchery-reared steelhead might affect the wild rainbow trout in the Yakima River system with respect to food habits. Wild and hatchery-reared fish were collected in the field by electro-fishing. Stomach contents were removed and preserved in the field for later analysis. Results indicate that hatchery-reared and wild fish have similar food habits, with Ephemeroptera, Trichoptera, and aquatic Diptera being the major prey items. Based on these results, it appears that any hatchery-reared steelhead smolts that residualize in the stream may compete for food items if food becomes a limiting resource.

FLOWERING AND VEGETATIVE PHENOLOGY OF THE BLACK COTTONWOOD (POPULUS TRICHOCARPA) IN THE WILLAMETTE VALLEY, OREGON. David H. Wagner, University of Oregon, Eugene.

A stand of 49 females and 47 males of black cottonwood (Populus trichocarpa) along the Willamette River was observed at approximately 10-day intervals, in 1987 and 1988, during periods of flowering, fruit maturation, leaf-out, and leaf-drop. Flowering and leaf-out are closely correlated but there is great variation in phenological patterns among individuals. The difference in timing was as great as five weeks between extreme individuals. Early trees had finished flowering and were fully leafed out before bud burst on the late ones. Similarly, in the fall some had dropped all leaves while others still had green leaves. Each individual, however, was generally consistent in its timing from year to year. Those that flowered and leafed out late also dropped their leaves late. Females began flowering later than the males, some not starting to flower until after all males in the stand had dropped their catkins.

THE GENUS PORELLA IN OREGON. David H. Wagner, University of Oregon, Eugene.

There are presently five species of Porella known from Oregon. The most common is P. navicularis, a western North American endemic. It occurs in the driest habitats of all leafy liverworts, exposed rocks and oak trunks, as well as a variety of other sites. Its morphological variability matches its ecology and odd forms are often misidentified as P. platyphylla which does not occur in the region. Porella roellii is another endemic, also very common, occurring in moister sites. Its peppery taste, when fresh, distinguishes it. Third in abundance is P. cordaeana, found also in Europe. It is frequently sub-aquatic. Porella bolanderi barely reaches southern Oregon, being mainly Californian. It looks much like a very dense-leaved P. cordaeana. The rarest of our scalemosses is the east Asian P. fauriei, collected only once, in the Columbia River Gorge, in 1920. It is probably acrid tasting. New illustrations and keys can supplant the faulty ones of Frye and Clark.

EVIDENCE FOR LONGITUDINAL WAVES IN PLANTS AND ELSEWHERE (W-WAVES). Q.E. Wagner, Wagner Research Lab., Rogue River, OR 97537.

I and others have found much evidence for heretofore elusive, matter and space penetrating, charge separating longitudinal waves. Some of the evidence is: (1) Anomalous charge separation voltages in plants and e.g. rocks with sinusoidal variation characteristics (2) Coincidences such as those reported by J. Weber in early results first thought to be associated with gravity waves. (3) Quantization of plant spacings with unique frequencies (such as 1.6 Hz, 0.6 Hz, and 2.666 Hz harmonics) associated with specific plant spacings. (4) The measurement of the same frequencies with low frequency spectrum analyzers. (5) Large charge separations (as evidenced by large voltage and current outputs dependent on the time of day) in insulated diode dies placed in light free slits in trees. (7) Diurnal changes in the apparent acceleration of gravity as indicated by very small accelerometers placed in small holes in the xylem of trees. Control accelerometers in dry dead wood indicate no such acceleration changes. See my articles and book "W-Waves and A Wave Universe" for more details.

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CAREX WORKING GROUP AT OREGON
STATE UNIVERSITY

Barbara Wilson, D. H. Norris,
and Peter F. Zika

A newly organized group of about eight individuals is beginning a long-term study of Carex in the state. Herbarium quality material is solicited, and the project members will identify selected collections. Long-term goals are high-resolution distribution maps for all Oregon species, and creating effective identification keys.

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COMPONENTS OF VEGETATION CHANGE
DURING TEN YEARS AFTER TEPHRA
BURIAL AT MOUNT ST. HELENS. Donald
B. Zobel, Oregon State University,
Corvallis. Joseph A. Antos, Univer-
sity of Victoria, Victoria, Canada.

Understory plant density and cover were determined in permanent plots buried by 4-14 cm tephra in 1980. The forest canopy remained intact. The degree of damage and recovery varied among growth forms and sites, but not among community attributes (species richness, cover, and density). Initial damage was least for shrubs and most for bryophytes; it was greatest where deep tephra had fallen on snow. The amount of change in attributes during a decade did not vary among sites and varied little among growth forms. Thus, the degree of recovery of pre-eruption values varied similarly to the pattern of damage. After ten years' recovery, surviving tree seedlings had reached equilibrium short of full recovery for most attributes, and bryophytes, for some; herbs reached equilibrium only where they had recovered in shallow tephra; for shrubs, only cover continued to increase.

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THE USFS'S UNSOUND PROCEDURE FOR
DETERMINING THE CUMULATIVE EFFECTS
OF LAND-USE ON SALMON AND AN
ALTERNATIVE APPROACH: "ENOUGH IS
ENOUGH." Jonathan J. Rhodes, Columbia River
Inter-Tribal Fish Commission, Portland, OR.

A sound method of assessing cumulative effects is an essential resource management tool. It is also mandated by a variety of federal laws. A sound cumulative effects approach must incorporate the effect of existing habitat conditions on salmon survival and identify where adverse cumulative effects already exist. It must also adequately integrate the effect of watershed conditions in combination with proposed activities on habitat. The USFS's proposed process fails to credibly incorporate these necessary components. In a variety of ways, it also consistently and significantly underestimates the severity of the cumulative effects on salmon survival. Use of the method will perpetuate the type of land management which has already degraded habitat and severely reduced salmon survival throughout the Columbia. An alternative approach is to thoroughly examine linkages among habitat conditions, the biological requirements of salmon, watershed conditions, and component landscape processes. In highly degraded areas, enough is enough, already.

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August 1993

Volume 67, Number 3

NORTHWEST SCIENCE

SMALL MAMMAL
DIVERSITY IN FORESTS



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Announcements

Annual Meeting of the Northwest Scientific Association

The 67th Annual Meeting of the Northwest Scientific Association will be held on March 24-26, 1994, at Central Washington University in Ellensburg, Washington. Other organizations are expected to participate in the meeting, including the Northwest Lichen Guild, Rare Plant Consortium, Society for Northwestern Vertebrate Biology, and the Association of Washington Geographers.

Three symposia have been proposed that are relevant to scientists and resource managers in the Pacific Northwest. These symposia will focus on: research in forest canopies, the Yakima River and associated resources, and the ecology and management of bull trout. The meeting will also have several sections for contributed papers. The first call for papers will be issued in October 1993. In addition, several field trips will be led by local scientists. Pat O'Hara, renowned wildlife and nature photographer, will be the guest speaker at the banquet, and give a presentation on the Beringian Heritage International Park.

All those interested in science and resource management issues in the Pacific Northwest are invited to attend. Students are especially encouraged to attend and participate in invited paper sessions. Special efforts will be made to reduce costs for student attendees. If you have additional ideas for the meeting or would like more information about it, please contact Dr. Ken Hammond, Department of Geography, Central Washington University, Ellensburg, WA 98926 (USA); telephone 509-963-1187; fax 509-963-1047.

Book Reviews in *Northwest Science*

Book reviews have been a periodic feature in *Northwest Science* for many years. Readers have indicated that they find the reviews to be quite useful, so I would like to make reviews a regular feature in future issues. If you see a new book that you think should be brought to the attention of the multidisciplinary readership of *Northwest Science*, please let me know, and I will try to arrange to have it reviewed.

—The Editor

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Influence of Vapor Pressure Deficit and Soil Moisture on Gas Exchange of *Juniperus occidentalis*

Abstract

An unusual combination of meteorological events allowed comparison of gas exchange for juvenile and adult *Juniperus occidentalis* under contrasting conditions of soil moisture and vapor pressure during August 1987 and August 1988. Responses of carbon dioxide assimilation, leaf conductance, transpiration, and intercellular carbon dioxide concentrations to changes in photosynthetic photon flux density, leaf temperature, and xylem water potential were measured for juvenile and adult trees. Carbon dioxide assimilation was significantly higher for juveniles with high soil water. Adult assimilation and conductance for both juveniles and adults were not significantly different in 1987 and 1988. Similar diurnal curves of leaf conductance in 1987 and 1988 were associated with different amounts of transpiration because of high vapor pressure deficits in 1987 and low soil water in 1988. Although stomata of juvenile *J. occidentalis* were more responsive than adult stomata, juveniles did not restrict transpiration when vapor pressure deficits were high; adults had higher water-use-efficiencies. With vapor pressure deficits > 3.5 kPa, fluctuations in leaf conductance of juvenile *J. occidentalis* indicated stomatal closure and reopening in ~ 20 minute cycles from 1000 to 1630 hr. Increases in air temperatures and vapor pressure deficits can be expected to have less effects on physiological processes of *J. occidentalis* than would variations in available soil moisture.

Introduction

Scenarios of future climatic change predict increasing air temperatures with concomitant increases in water vapor pressure deficits experienced by plants; patterns of precipitation and soil moisture are also predicted to change (Schlesinger and Mitchell 1987, Hansen *et al.* 1988, Manabe and Wetherald 1987). In a localized region, increased air temperatures may or may not be accompanied by decreased precipitation and soil moisture (Manabe and Wetherald 1987, Running and Nemani 1989). Information on the response of naturally established trees to unusual, but natural, combinations of soil moisture and vapor pressure deficits can provide insight as to which environmental factors are most limiting and how native species may respond to predicted alterations of climatic regimes.

An unusual precipitation event ($P < 0.001$) during July, 1987, produced 95 mm of precipitation at Redmond, OR, compared to the average July precipitation of 7.4 mm (NOAA 1982). During August 1987, a period of high air temperatures and high water vapor pressure deficits occurred while soil water content was higher ($P < 0.10$) than was soil water content during August, 1988, a summer with precipitation similar to the long term average at Redmond (NOAA 1982). Soil moisture was unusually high for almost a month prior to the

August 1987 measurements and was low for the month prior to the August 1988 measurements. This month long period of preconditioning allowed the trees used in this research to equilibrate with soil moisture conditions.

Mean maximum and mean minimum air temperatures were similar for the month preceding the measurements in 1987 and 1988 (Miller *et al.* 1992). However, the extreme maximum air temperature of 42.5°C on 10 Aug 87 was considerably above the highest August mean maximum air temperature of $30 \pm 3.6^{\circ}\text{C}$ measured at Redmond, OR, from 1951 to 1980 (NOAA 1982). This combination of unusual precipitation and extreme air temperature produced experimental conditions that allowed comparison among *Juniperus occidentalis*, which were in a similar phenological stage at the same field site, under contrasting environmental regimes of high soil moisture and high vapor pressure deficits in August, 1987, versus low soil moisture and relatively low vapor pressure deficits in August, 1988.

Data for the two August periods, which focused on small trees with juvenile foliage and large trees with adult foliage, were part of a larger 15 month study on the seasonal course of physiological processes for *J. occidentalis* (Miller *et al.* 1992). Analysis of the two August data sets indicated contrasting patterns of physiological responses that provided the opportunity to explore the plasticity

of naturally established trees by focusing on a detailed analysis and comparison of diurnal responses of juvenile and adult trees. Presentation of this type of detailed analysis was not possible for the total 15 month data set. The two August periods were chosen because they contained interesting contrasts in plant responses to differing environmental conditions.

Juniperus occidentalis Hook. subsp. *occidentalis* is a native North American conifer that has spread and increased in density in eastern Oregon during the last 100 years (Dealy *et al.* 1978). Under the present climatic regime, *J. occidentalis* currently occupies 1,145,000 ha in central Oregon (Dealy *et al.* 1978); it has successfully invaded non-degraded communities and communities degraded by grazing animals and by fire suppression (Young and Evans 1981). The tolerance of *J. occidentalis* to low soil moisture and high vapor pressure deficits may determine its ability to withstand increases in air temperatures and decreases in precipitation predicted with increased levels of greenhouse gasses and may effect its ability to continue to spread and increase in density in eastern Oregon.

Objectives of this research were to measure the response of carbon dioxide assimilation, leaf conductance, and intercellular carbon dioxide concentrations to changes in photosynthetic photon flux density, leaf temperature, and xylem water potential as the result of contrasting combinations of soil moisture and ambient vapor pressure deficits.

Methods

The research site, located 12.8 km west of Redmond, Oregon (44° 16' N, 121° 20' W), is a gentle, west-facing slope at 1050 m elevation. The soil is a well drained loamy-skeletal, Aridic Haploxeroll derived from Mazama volcanic ash over tuff, with a uniform silty loam texture down to a hard pan at about 70 cm. Annual precipitation at Redmond averages 217 mm, 89% of which occurs from October to June (NOAA 1982). The plant community at the research site was similar to the *Juniperus/Artemisia/Agropyron-Chaenactis* association described by Driscoll (1964).

Juniperus occidentalis has needle-like juvenile leaves which are replaced by scale-like adult leaves as the plant matures (de Laubenfels 1953). Trees with only juvenile foliage may be up to 26 yrs old and over 1 m tall (Miller *et al.* 1990). Two juveniles

and 2 adults were measured in 1987 and 4 juveniles and 4 adults in 1988. Juveniles had 100% juvenile foliage and were 30 to 60 cm tall; the estimated height of adults was 4 to 4.5 m. Juveniles large enough to support diurnal sampling were located first and adults growing near-by were selected, based on proximity and the requirement that the south side of the tree be in full sun through the day. Branchlets used for physiological measurements were on the south side of the tree, 10 cm to 1.5 m above the ground surface.

Diurnal measurements of physiological processes were made on 8 and 10 August 1987 and on 2 and 3 August 1988. This paper will focus on 10 August 1987 when each tree was measured 36 times during the day with conditions of high soil moisture and high vapor pressure deficits (H) and on 2 August 1988 when each tree was measured 15 times with conditions of low soil moisture and low vapor pressure deficits (L).

Carbon dioxide assimilation and relative humidity were measured using an Analytical Development Corporation LCA-2 portable infrared gas analyzer system and a PLC(C) Parkinson leaf chamber with a volume of 137 cm³. Leaf conductance, transpiration, intercellular carbon dioxide concentrations, and water vapor pressure deficits inside the cuvette were calculated. Photon flux density (400-700 nm) was measured with a LiCor 190 SB quantum sensor; leaf and air temperatures were measured with fine gauge copper/constantan thermocouples and a Campbell Scientific CR 10 data logger. Vapor pressure deficits in the cuvette were calculated using leaf temperatures measured in the cuvette. Xylem water potentials were measured with a PMS Instruments pressure chamber. Data were reduced using a BASIC program (Miller 1990) based on equations from Wexler (1976, 1977), Nobel (1983), Campbell (1986), and Ball (1987). Soil moisture was measured gravimetrically during each measurement period (Hillel 1971).

Similar amounts of foliage tissue were used for gas exchange measurements in both years; dry mass of juvenile foliage was 0.3458 g in 1987 and 0.3326 g in 1988; dry mass of adult foliage was 0.5115 g in 1987 and 0.5052 g in 1988. The tissue was produced during the period of rapid branchlet elongation from May through early August (Miller *et al.* 1992). The same tissue was measured repeatedly throughout the day. Carbon dioxide assimilation, leaf conductance, and transpiration data were presented on a dry mass basis

because measurements of dry mass were considered more accurate than leaf area measurements (Miller *et al.* In prep). Daily totals of carbon dioxide assimilation per gram of foliage were calculated by integrating under measured diurnal curves.

Significance of differences between a single observation and a sample mean was determined using a special case of the Student's *t*-test (Sokal and Rohlf 1981). Diurnal response curves of physiological processes between years were compared using two-tailed Mann-Whitney tests (Zar 1984, Potvin *et al.* 1990). For each Mann-Whitney test, the data on one process, i.e., carbon dioxide assimilation for juvenile *J. occidentalis* in 1987 and in 1988, were ranked; a separate test was used to compare the same process for large-adults in 1987 and in 1988. Statistical significance levels were set at $P < 0.05$, but probabilities levels greater than 0.05 are reported because biological significance and statistical significance are not always synonymous.

Results

During the four month period prior to the August measurements, precipitation at Redmond, OR, was 146 mm in 1987 and 63 mm in 1988: the average precipitation for April through July is 63 mm at Redmond (NOAA 1982). Gravimetric soil water content was higher on 10 Aug 87 than 2 Aug 88 ($P < 0.10$). Water contents at 0-5, 10-15, 25-30, and 45-50 cm depths were 1.53, 9.2, 11.1, and 7.5% on 10 Aug 87 and 0.8, 4.2, 5.4, and 6.1% on 2 Aug 88.

Diurnal curves of photosynthetic photon flux density ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$, *PFD*) on 10 Aug 87 and 2 Aug 88 were similar, but daytime air temperatures and water vapor pressure deficits were significantly higher during the 10 Aug 87 measurement period ($P < 0.003$ and 0.05, respectively) (Fig. 1A). Leaf temperatures for juvenile and adult *J. occidentalis* in the cuvette were also significantly higher on 10 Aug 87 than 2 Aug 88 ($P < 0.03$, and < 0.05 , respectively). During the 10 Aug 87 measurements, maximum leaf temperatures were $> 35^\circ\text{C}$ and water vapor pressure deficits in the cuvette were $> 4 \text{ kPa}$ from 1130 to 1600 hr.; while on 2 Aug 88 maximum leaf temperatures were $< 33^\circ\text{C}$. through the day and water vapor pressure deficits in the cuvette were $> 4 \text{ kPa}$ only from 1430 to 1530 hr (data not shown). The letters H and L will be used to remind the

reader that soil moisture and vapor pressure deficits were high on 10 Aug 87 and low on 2 Aug 88.

The highest rates of carbon dioxide assimilation, $17.2 \text{ nmol g}^{-1} \text{s}^{-1}$, were measured for juvenile *J. occidentalis* on 10 Aug 87 (H). Diurnal curves of assimilation for juveniles was significantly higher on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.02$) (Fig. 1B), and daily total carbon dioxide assimilation was 71% higher on 10 Aug 87 (H) than on 2 Aug 88 (L), $425 \mu\text{mol g}^{-1} \text{d}^{-1}$ versus $248 \mu\text{mol g}^{-1} \text{d}^{-1}$.

The highest carbon dioxide assimilation for adults, $10.5 \text{ nmol g}^{-1} \text{s}^{-1}$ was also measured on 10 Aug 87 (H), but the highest rate for 2 Aug 88 (L) was only slightly lower, $10.1 \text{ nmol g}^{-1} \text{s}^{-1}$. Statistical tests did not indicate a significant difference in diurnal curves of assimilation in adults on 10 Aug 87 (H) and 2 Aug 88 (L) because rates during the morning were similar (Fig. 1B). However, during the afternoon of 10 Aug 87 (H) carbon dioxide assimilation remained at levels similar to those measured during the morning; on 2 Aug 88 (L) assimilation declined steadily after 1200 h. Therefore, total daily carbon dioxide assimilation for adults was 25% greater on 10 Aug 87 (H) than on 2 Aug 88 (L), $356 \mu\text{mol g}^{-1} \text{d}^{-1}$ versus $284 \mu\text{mol g}^{-1} \text{d}^{-1}$.

Diurnal curves of intercellular carbon dioxide concentrations (c_i) for juvenile and adult *J. occidentalis* were significantly lower on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.002$ and 0.001, respectively). In both years, the lowest c_i were measured for adults, $282 \mu\text{mol}$ on 10 Aug 87 (H) and $308 \mu\text{mol}$ on 2 Aug 88 (L) (Fig. 1c).

Patterns of the response of carbon dioxide assimilation to the diurnal course of photosynthetic photon flux density, 400-700 nm (*PFD*) for juvenile *J. occidentalis* (Fig. 2A) were more dissimilar on 10 Aug 87 (H) and 2 Aug 88 (L) than were the patterns for adults during the two measurement periods (Fig. 2B). The high juvenile assimilation rates measured on 10 Aug 87 (H) were not present with similar levels of *PFD* on 2 Aug 88 (L). Adult carbon dioxide assimilation was similar in the morning in both years, but no afternoon hysteresis occurred on 10 Aug 87 (H); therefore, the response of assimilation to *PFD* for adult *J. occidentalis* was similar in the morning and afternoon during 10 Aug 87 (H).

Carbon dioxide assimilation for juvenile *J. occidentalis* was 80% of maximum with leaf

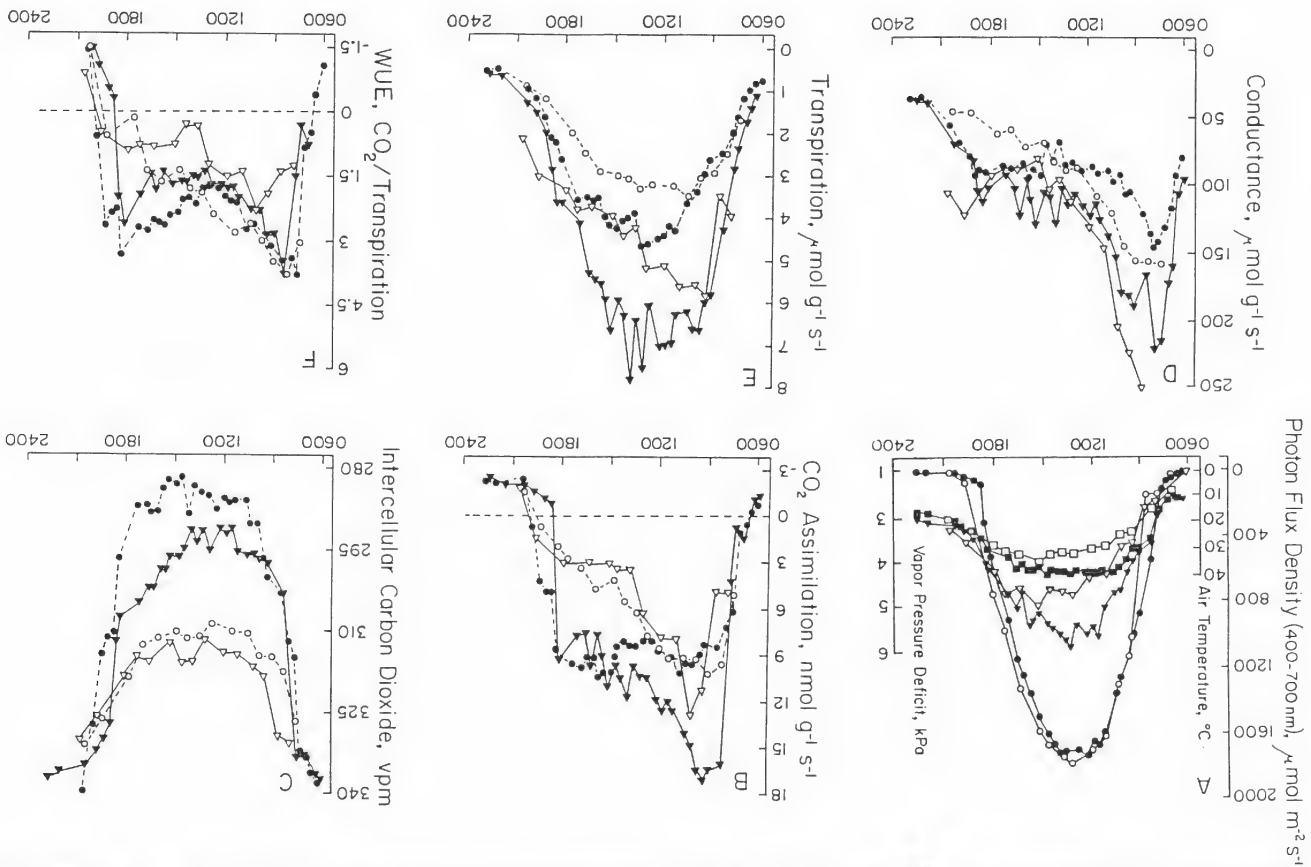


Figure 1. The diurnal course of (A) photosynthetic photon flux density (400-700 nm) ($\mu\text{mol m}^{-2} \text{s}^{-1}$) on August 10, 1987 (●) and August 2, 1988 (○), of air temperature ($^{\circ}\text{C}$) Aug 10-87 (■) and Aug 2-88 (□), and of vapor pressure deficit (kPa) Aug 10-87 (▲) and Aug 2-88 (△). The diurnal course of (B) carbon dioxide assimilation, (C) intercellular carbon dioxide, (D) leaf conductance, (E) transpiration, and (F) water use efficiency (WUE) of juvenile *J. occidentalis* on Aug 10-87 (▲) and Aug 2-88 (△) and of adults on Aug 10-87 (●) and Aug 2-88 (○).

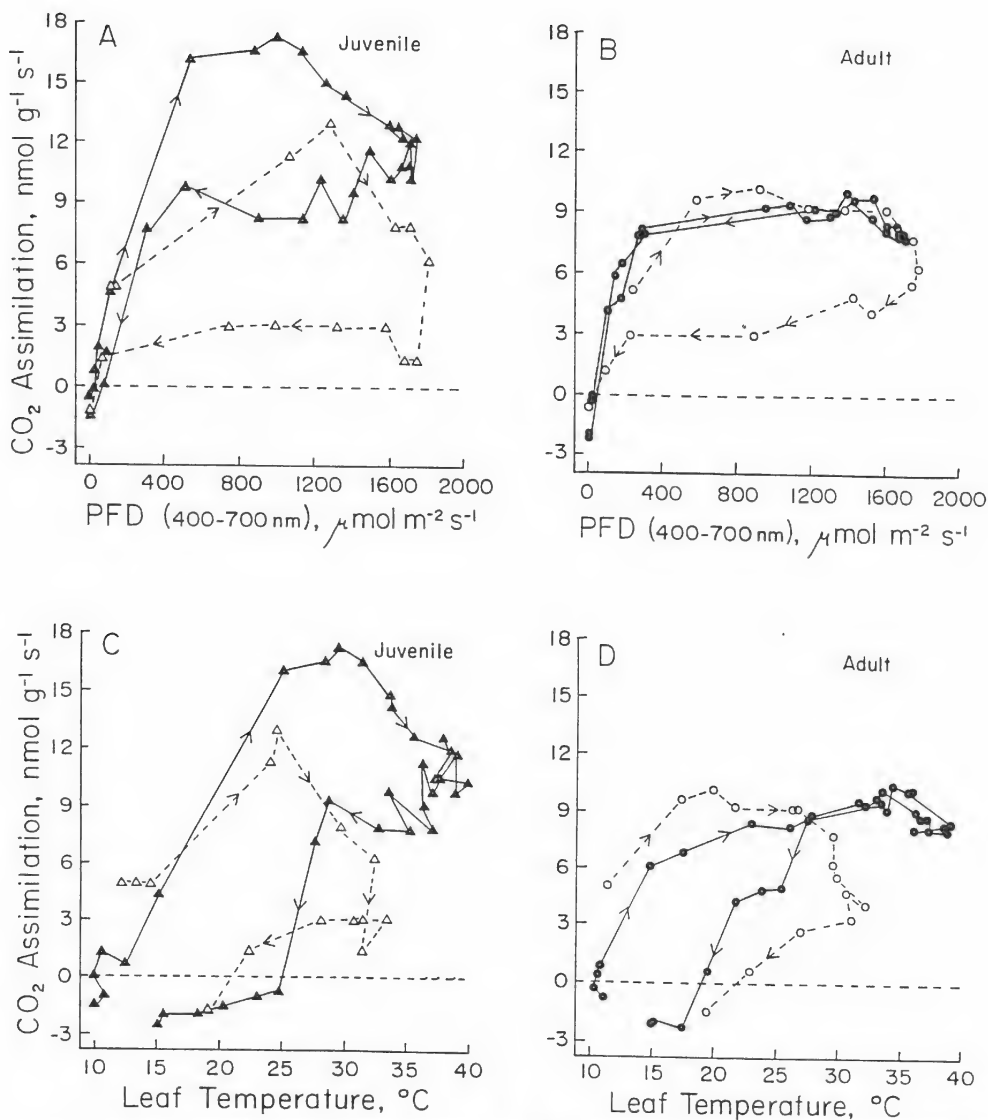


Figure 2. The diurnal course ($\rightarrow$) of carbon dioxide assimilation (nmol g⁻¹ s⁻¹) as a function of (A and B) photon flux density (400-700 nm PFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and (C and D) leaf temperature (°C) of juvenile *J. occidentalis* on Aug 10-87 (Δ) and Aug 2-88 ($\blacktriangle$) and of adults on Aug 10-87 ($\circ$) and Aug 2-88 ($\bullet$).

temperatures of 23-34.5 °C on 10 Aug 87 (H) (Fig. 2C) and with temperatures of 23-27 °C on 2 Aug 88 (L) (Fig. 2D). For adults, assimilation was 80% of maximum over a broader range of leaf temperatures, 22-39 °C on 10 Aug 87 (H) and 15-29 °C on 2 Aug 88 (L).

Maximum leaf conductances (stomatal plus cuticle and boundary layer) for juveniles were 222 and 253 $\mu\text{mol g}^{-1} \text{s}^{-1}$ on 10 Aug 10 (H) and 2 Aug 88 (L), respectively; maximum conductances for adults were 145 and 157 $\mu\text{mol g}^{-1} \text{s}^{-1}$ for the two August measurements (Fig. 1D). Diurnal leaf

conductance curves for juvenile and for adult *J. occidentalis* were similar during the two years; however, juvenile diurnal transpiration was significantly higher on 10 Aug 87 (H) than on 2 Aug 88 (L) ($P < 0.02$) (Fig. 1E) as the result of differences in vapor pressure deficit (Fig. 1A). Transpiration for adults was also higher on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.16$) (Fig. 1E). Total daily transpiration was 35% higher for juvenile *J. occidentalis* on 10 Aug 87 (H) than 2 Aug 88 (L), 252 $\text{mmol g}^{-1} \text{d}^{-1}$ versus 187 $\text{mmol g}^{-1} \text{d}^{-1}$, and 32% higher for adults, 162 $\text{mmol g}^{-1} \text{d}^{-1}$ versus 122 $\text{mmol g}^{-1} \text{d}^{-1}$.

The diurnal pattern of leaf conductance plotted against water vapor pressure deficits for juvenile and adult *J. occidentalis* on 10 Aug 87 (H) indicated a pattern of stomatal closure and reopening during approximately 20 minute cycles from 1100 to 1630 hr (Fig. 3A and 3B), when water vapor pressure deficits were > 3.5 kPa. On 2 Aug 88 (L), leaf conductance declined more rapidly over a narrower range of water vapor pressure deficits and the pattern of cyclical stomatal closure was less pronounced than on 10 Aug 87 (H) (Fig. 3A and 3B).

Xylem water potentials for juvenile and adult *J. occidentalis* were significantly less negative throughout the day on 10 Aug 87 (H) than 2 Aug 88 (L) ($P < 0.001$ and 0.003, respectively). Pre-dawn and mid-day xylem water potentials were -0.5 and -2.2 MPa and -0.4 and -1.95 MPa, respectively, for juvenile and adult *J. occidentalis* on 10 Aug 87 (H). On 2 Aug 88 (L) pre-dawn and mid-day potentials were -2.4 and -4.1 MPa for juvenile and -2.0 and -3.3 for adult trees.

On 10 Aug 87 (H), the diurnal response of leaf conductance to whole plant water status, as measured by xylem water potentials, indicated repeated stomatal closure and reopening within a narrow range of xylem water potentials, -1.6 to -2.2 MPa for juvenile (Fig. 3C) and -1.1 to -1.95 MPa for adult *J. occidentalis* (Fig. 3D). The range of conductance values on 2 Aug 88 (L) was similar to the range measured on 10 Aug 88 (H) for both juvenile and adult *J. occidentalis*, but oscillations were not observed on 2 Aug 88 (L).

Juvenile water-use efficiency (carbon dioxide assimilation/transpiration, *WUE*) was significantly higher on 10 Aug 87 (H) than on 2 Aug 88 (L) ($P < 0.001$) (Fig. 1F). On 10 Aug 87 (H) adult *WUE* had a bimodal pattern with peaks in the

morning and afternoon; on 2 Aug 88 (L) adult *WUE* declined steadily throughout the day (Fig. 1F), but the diurnal curves were not significantly different ($P < 0.24$).

Discussion

Physiological processes for juvenile *J. occidentalis* in eastern Oregon were more responsive to environmental conditions than were similar processes for adult trees. Carbon dioxide assimilation for juveniles varied 71% more with the measured range of *PDF* and 74% more with the measured range of leaf temperatures than did assimilation for adults. Leaf conductance for juveniles was 39% and 26% more variable with the measured range of vapor pressure deficits and xylem pressure potentials than was conductance for adults.

The lack of hysteresis in the response of adult *J. occidentalis* assimilation to *PFD* on 10 Aug 87 (H) indicated that, with adequate soil moisture, high rates of adult carbon dioxide assimilation were maintained throughout the day, declining only when light levels were below $300 \mu\text{mol m}^{-2} \text{s}^{-1}$.

The similarity of diurnal curves of conductance on 10 Aug 87 (H) and 2 Aug 88 (L) in both juvenile and adult *J. occidentalis* indicated a similar degree of stomatal opening on both days despite differences in soil water and vapor pressure deficits during the two August periods. Daily transpirational loss of water appeared to be controlled more by environmental conditions of soil moisture availability and vapor pressure deficit than by the physiological mechanism of stomatal opening and closing.

The cyclical response of juvenile *J. occidentalis* conductance on 10 Aug 87 (H) when *VPD* was > 4 kPa may indicate a feed forward response of stomata (Cowan 1977, Farquhar 1978) to high vapor pressure deficits or may be caused by an overshoot in leaf water content or by CO_2 feedback loops controlling stomatal aperture (Weyers and Meidner 1990). However, cycles of stomatal closure on 10 Aug 87 (H) were not sufficient to reduce carbon dioxide assimilation or transpiration of juvenile *J. occidentalis*. Integrating under the 10 Aug 87 (H) diurnal curves with and without the reductions resulting from stomatal closure indicated only a 5% reduction in daily assimilation and a 3% reduction in transpiration due to stomatal closure. The cycle pattern of juvenile stomatal closure was not evident on 2 Aug 88 (L) even though

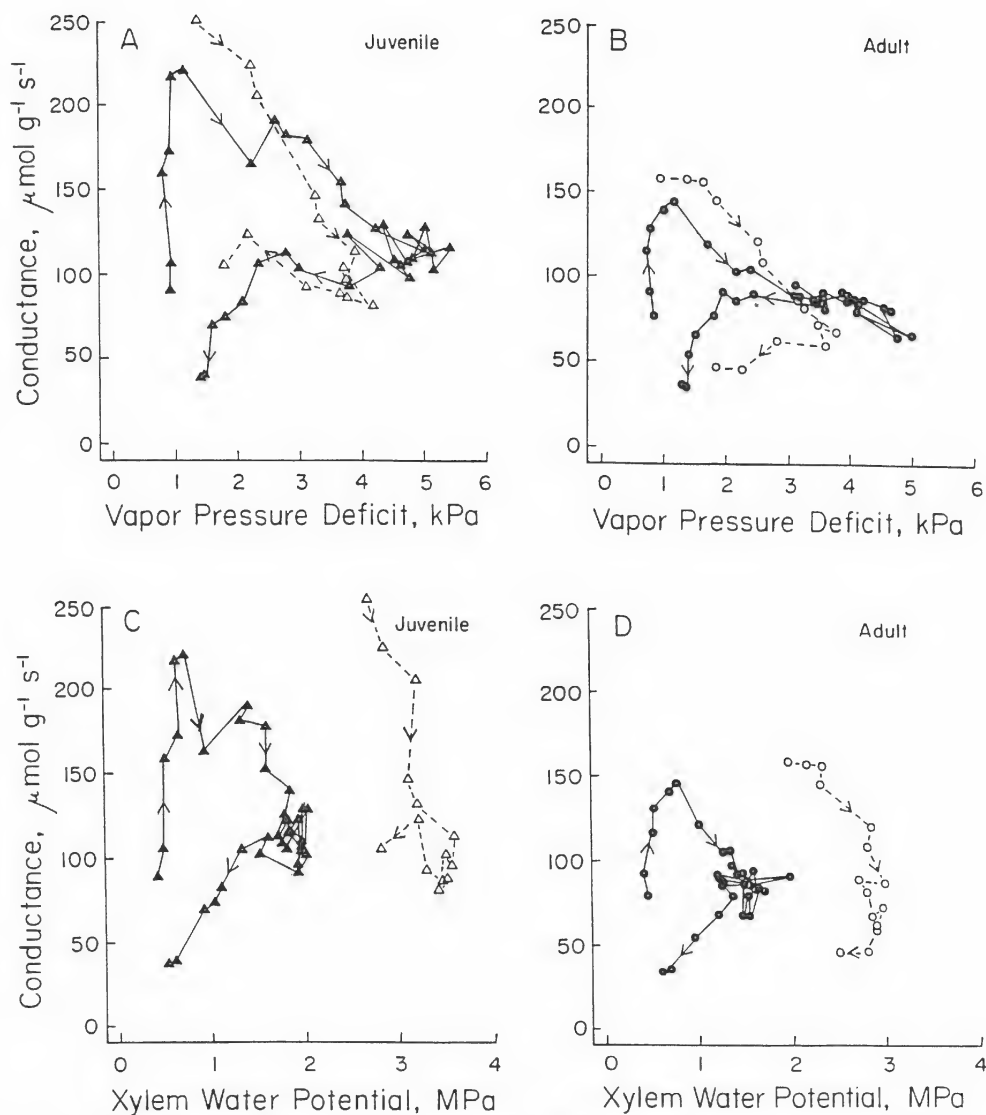


Figure 3. The diurnal course ($\rightarrow$) of leaf conductance ($\mu\text{mol g}^{-1} \text{s}^{-1}$) with (A and B) vapor pressure deficit (kPa) and (C and D) xylem water potential (MPa) of juveniles *J. occidentalis* on Aug 10-87 ($\blacktriangle$) and Aug 2-88 ($\triangle$) and of adults on Aug 10-87 ($\bullet$) and Aug 2-88 ($\circ$).

the average soil moisture at 0-50 cm depth was 44% lower and pre-dawn xylem pressure potentials were almost 5x more negative than on 10 Aug 87 (H).

Stomata of adult *J. occidentalis* did not appear to have the same feed forward response to vapor

pressure deficits as was measured in juveniles. Location of adult leaf stomata on the adaxial surface, not exposed to air movement, and on the abaxial surface, covered by the adjacent scale leaf (Miller and Shultz 1987), may reduce the sensitivity of the response of adult leaf conductance to high vapor pressure deficits.

An additional trigger for stomatal closure may be generated by a regulatory coupling of the rate of foliar water loss with the moisture environment of roots (Bates and Hall 1981, Gollan *et al.* 1985). Differences in the response of leaf conductance to high vapor pressure deficits in juvenile and adult *J. occidentalis* on 10 Aug 87 (H) may be related to the larger volume of soil available for water extraction by the extensive root system of adult *J. occidentalis*. Water supply from adult roots may have kept up with evaporative demand on 10 Aug 87 (H), while signals from the smaller juvenile root system triggered cyclical stomatal closure to more closely balance supply and demand. Therefore, the cyclical patterns of stomatal closure and resulting fluctuations in carbon dioxide assimilation and conductance were less pronounced in adults than juveniles on 10 Aug 87 (H). Reich and Hinckley (1989) concluded that leaf conductance of *Quercus marilandica* and *Quercus rubra* was controlled by root or soil water potential and speculated that differences in their fine roots systems or cavitation affected plant hydraulic conductance when soils were dry.

Although stomata of juvenile *J. occidentalis* were more responsive than adult stomata to vapor pressure deficits and xylem water potentials, juveniles did not restrict transpiration when vapor pressure deficits were high. Assimilation rates of juveniles were not high enough to compensate for their high transpiration; adult *J. occidentalis* with less responsive stomata and lower rates of assimilation had higher *WUE* on 10 Aug 87 (H) than did juveniles.

It has been suggested that carbon dioxide assimilation and leaf conductance do not respond in parallel to temperature (Morison 1987). In *Agropyron desertorum*, conductance did not change greatly with leaf temperature, so changes in assimilation rates were attributed to direct effects of temperature (Nowak *et al.* 1988). On 10 Aug 87 (H), the correlation between assimilation and leaf temperature was stronger for juvenile and adult *J. occidentalis* ($r^2 = 0.58$ and 0.71 , respectively) than was the correlation between leaf conductance and leaf temperature ($r^2 = 0.02$ and 0.005 , respectively). However on 2 Aug 88 (L), the pattern was reversed; the correlation between carbon dioxide assimilation and leaf temperature for juvenile and

adults was low ($r^2 = 0.0005$ and 0.004 , respectively), and the correlation between leaf conductance and leaf temperature was higher ($r^2 = 0.66$ and 0.36 , respectively). For *J. occidentalis* the effects of temperature on assimilation and leaf conductance appears to be influenced by soil moisture availability, but high leaf temperatures of up to 39°C did not appear to have a direct effect on assimilation.

Processes of carbon dioxide assimilation and leaf conductance do not appear to be strongly coupled in juvenile and adult *J. occidentalis* at the research site in eastern Oregon; they responded independently to variations in air temperature, vapor pressure deficits, and soil moisture. The positive effect of high soil water in August was a more important factor influencing carbon dioxide assimilation in *J. occidentalis* than were the negative effects of vapor pressure deficits > 4 kPa on stomatal closure and leaf conductance.

Conclusions

Juvenile and adult *J. occidentalis* in eastern Oregon are able to tolerate a wide range of leaf temperatures and vapor pressure deficits. Periods of above average temperatures and vapor pressure deficits, if associated with adequate soil moisture, should not adversely affect their physiological processes. Established adult trees are more buffered against variations of soil moisture than are juveniles. The responsiveness of juvenile *J. occidentalis* to soil moisture is advantageous under favorable conditions. However, the depression of juvenile assimilation and the relative inability of their stomata to restrict water loss when soil water resources are limited may reduce their establishment, competitive ability, and the spread of *J. occidentalis* in eastern Oregon during periods of reduced precipitation.

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Literature Cited

- Ball, J. T. 1987. Calculations related to gas exchange. P.445-476 in E. Zeiger, G. D. Farquhar and I. R. Cowan (eds.), Stomatal function. Stanford University Press, Stanford, CA.
- Bates, L. M. and A. E. Hall. 1981. Stomatal closure with soil water depletion not associated with changes in bulk leaf water status. *Oecologia* (Berlin) 50:62-65.
- Campbell G. S. 1986. An introduction to environmental biophysics. Springer-Verlag, New York, NY.
- Cowan, I. R. 1977. Stomatal behavior and environment. *Adv. Bot. Res.* 4:117-228.
- Dealy, J. E., J. M. Geist, and R. S. Driscoll. 1978. Western juniper communities on rangelands of the Pacific Northwest. P. 201-204 in D. N. Hyder (ed.), In First international rangeland congress. Soc. Range Mang. Denver, CO.
- de Laubenfels, D. J. 1953. The external morphology of coniferous leaves. *Phytomorphology* 3:1-17.
- Driscoll, R. S. 1964. Vegetation-soil units in the central Oregon juniper zone. USDA For. Ser. PNW Res. Pap. 19, Ogden, UT.
- Farquhar, G.D. 1978. Feedforward responses of stomata to humidity. *Aust. J. Pl. Phys.* 5:787-800.
- Gollan, T., N. C. Turner, and E.-D. Schulze. 1985. The responses of stomata and leaf gas exchange to vapor pressure deficits and soil water content. III. In the sclerophyllous woody species *Nerium oleander*. *Oecologia* (Berlin) 65:356-362.
- Hansen, J., I. Fung, A. Lacis, D. Rind, S. Lebedeff, R. Ruedy, and G. Russell. 1988. Global climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. *J. Geo. Res.* 93:9341-9364.
- Hillel, D. 1971. Soil and water, physical principles and processes. Academic Press, New York, NY.
- Manabe, S. and R. T. Wetherald. 1987. Large-scale changes of soil wetness induced by an increase in atmospheric carbon dioxide. *J. Atmos. Sci.* 44:1211-1246.
- Miller, P. M., L. E. Eddleman, and S. Kramer. 1990. Allocation patterns of carbon and minerals in juvenile and small-adult *Juniperus occidentalis*. *For. Sci.* 36:729-742.
- Miller, P. M., L. E. Eddleman, and J. M. Miller. 1992. The seasonal course of physiological processes in *Juniperus occidentalis*. *For. Eco. Manage.* 48:185-215.
- . Advantages and disadvantages of juvenile foliage in *Juniperus occidentalis*. In prep.
- Miller, R. F. and L. M. Shultz. 1987. Water relations and leaf morphology of *Juniperus occidentalis* in the northern Great Basin. *For. Sci.* 33:690-706.
- Morison, J. I. L. 1987. Stomatal response to CO₂. P. 228-251 in E. Zeiger, G. D.
- Farquhar, I. R. Cowan (eds.), Stomatal function. Stanford University Press, Stanford, CA.
- NOAA. 1982. Monthly normals of temperature, precipitation, and heating and cooling degree days 1951-1980 Oregon. National Climatic Center. Washington, D.C.
- Nobel, P. S. 1983. Biophysical plant physiology and ecology. W. H. Freeman and Co., San Francisco, CA.
- Nowak, R. S., J. E. Anderson, and N. L. Toft. 1988. Gas exchange of *Agropyron desertorum*: diurnal patterns and responses to water vapor gradient and temperature. *Oecologia* (Berlin) 77:289-295.
- Potvin, C., M. J. Lechowicz, and S. Tardif. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71:1389-1400.
- Reich, P. B. and T. M. Hinckley. 1989. Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance in two oak species. *Functional Ecology* 3:719-726.
- Rumming, S. W. and R. Nemani. 1989. Projecting the response of Montana forests to global climate change. *Bull. Eco. Soc. Am.* 70:250.
- Schlesinger, M. E. and J. F. B. Mitchell. 1987. Climate model simulations of the equilibrium climatic response to increased carbon dioxide. *Geo. Rev.* 25:760-998.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., San Francisco, CA.
- STSC Inc. 1987. Statgraphics® statistical graphics system. STSC Inc. Rockwell, MD.
- Wexler, A. 1976. Vapor pressure formulation for water in the range 0° to 100° c—A revision. *J. Res. Nat. Bur. Stand.* 80: 775-798.
- . 1977. Vapor pressure formulation for ice. *J. Res. Nat. Bur. Stand.* 81A:5-20. Washington, D.C.
- Weyers, J. D. B. and H. Meidner. 1990. Methods in stomatal research. Longman Scientific and technical, London, England.
- Young, J. A. and R. A. Evans. 1981. Demography and fire history of a western juniper stand. *J. Range Manage.* 34:501-505.
- Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.

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Jimmy L. Reaves,¹ Research Plant Pathologist, USDA Forest Service, Pacific Northwest Research Station, 3200 Jefferson Way, Corvallis, Oregon 97331

Charles G. Shaw III, Supervisory Research Plant Pathologist, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 240 West Prospect Street, Fort Collins, Colorado 80526

and

Lewis F. Roth, Professor Emeritus, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331

Infection of Ponderosa Pine Trees by *Armillaria ostoyae*: Residual Inoculum versus Contagion

Abstract

Infection of ponderosa pine roots by *Armillaria ostoyae* was evaluated in 17 excavations of disease centers conducted 14 and 15 years after stand regeneration on ground previously treated to remove *Armillaria* inoculum. Residual inoculum was the recognizable source of infection for the first 28 trees to die in 15 of the 17 new root disease centers; the other 76 affected trees in these centers became infected by contagion from the initially attacked trees. Dead and dying trees were girdled at the root collar by host resin and *Armillaria* mycelium and had most of their roots infected. *Armillaria*-caused lesions occurred on roots of dead and dying trees and also on trees lacking above-ground disease symptoms. On symptomatic trees, the fungus was not occluded within root lesions and spread both distally and proximally from them. In contrast, the fungus was occluded within distinct lesions on roots of trees lacking above-ground symptoms. These results verify that initial infections by *A. ostoyae* on regenerated ponderosa pines results from residual, primary inoculum that significantly functions for about 12 years. As with disease development in natural stands, subsequent infections and fungal spread that generates recognizable disease centers results from contagion. This information will assist forest managers contemplating initial control measures and their determining if any subsequent treatments are needed.

Introduction

Armillaria root disease, caused by *Armillaria ostoyae* (Romang.) Herink, is sometimes so severe in the Pacific Northwest that affected ponderosa pine (*Pinus ponderosa* Laws.) stands fail to produce commercial timber for decades (Hadfield *et al.* 1986, Hagle and Shaw 1991, Kile *et al.* 1991, Shaw *et al.* 1976, Wargo and Shaw 1985, Williams *et al.* 1989). Productivity of severely impacted sites might be restored through removing infected roots of the previous stand (Arnold 1981, Morrison *et al.* 1988, 1992; Redern and Filip, 1991, Roth and Shaw, unpublished) that serve as residual inoculum and sources of primary spread to a succeeding stand (Shaw 1980). This inoculum ranges in size from large, intact root systems and stumps to small roots and fungal rhizomorphs.

Irrespective of treatment technique, machine removal of inoculum (Arnold 1981, Bloomberg and Reynolds 1988) is not complete as generally some infected material remains. Through time, *A. ostoyae* and other organisms decompose this remaining inoculum and eventually render it ineffec-

tive, but not before some disease is transmitted by contact with roots of regenerated trees (Shaw 1980). Thus, follow-up treatment might be needed to secure the initial investment in sanitation and to sustain the health of the regeneration to a harvestable age.

The need and timing of any such follow-up treatments could be more accurately determined with better knowledge of the longevity of *A. ostoyae* in residual inoculum. Furthermore, information on the time at which significant roots of the regenerated stand (contagion) is needed—the information sought through this excavation study. Knowledge gained from this study will enhance our knowledge on the vegetative spread of the fungus and thus facilitate disease control decisions.

Methods

Study Area Description

Our observations were made in a 3.6 hectare stand of young ponderosa pine located at the north base of Meadow Butte (NE1/4, Sec 10, T6N, R11E) in south central Washington state, about 15 Km northwest of Glenwood (Figure 1). The previous stand of ponderosa pine on this site had been so severely damaged by *Armillaria* root disease that

¹Present Address: USDA Forest Service, Alabama A&M University, P. O. Box 1387, Normal, AL 35762

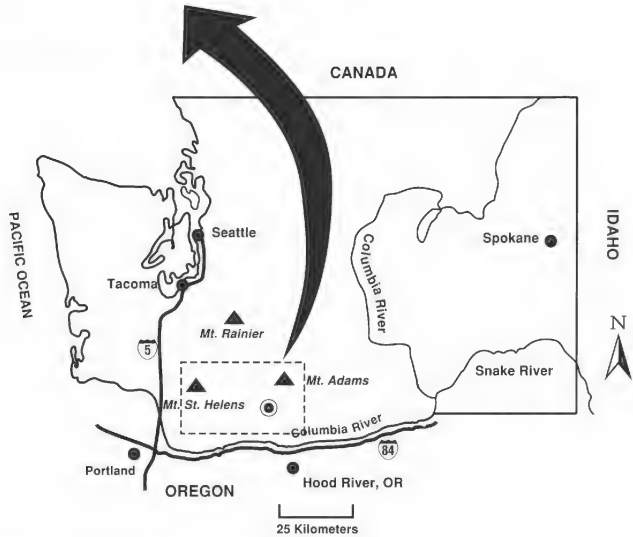
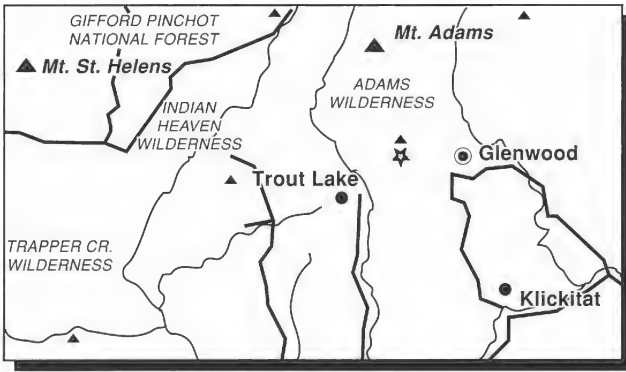


Figure 1. Location (star) of study area near Glenwood, Washington.

there was little likelihood of its persisting as a commercial, timber-producing forest (Shaw 1980, Shaw and Roth 1976, Shaw *et al.* 1976) (Figure 2). This location is part of the area that received recent attention from the nation's press during the "humongous fungus debate" (Ecenbarger 1992).

The stand was clear-cut in 1971, inoculum removed by bulldozer and raked, and the site allowed to regenerate naturally. In 1972, regeneration on the middle 1/3 of the area was destroyed and replaced with stock from Oregon and the local

source. Northern and southern thirds of the tract regenerated at natural stand densities. In 1977, trees in the middle and north thirds were thinned by pulling surplus trees to leave approximately 3113 trees/hectare.

During six of the ten years preceding death of the trees examined in this study, densities in the young stand had been somewhat reduced by annual removal of dead trees to measure effectiveness of the sanitation treatments (Roth and Shaw, unpublished). The work described here began



Figure 2. (A) A typical diseased stand located in the study area before *Armillaria ostoyae*-infected trees, snags, and stumps were removed by bulldozer; and (B) stand structure after approximately 13 years after disease treatments were administered.

after four years of not removing these dead trees, at which time mortality was present as either single trees or as small groups.

Excavation Procedure

Seventeen of these mortality groups, each with 3 or more dead trees and occupying an area ranging from 2–4 m², were evident in 1987. Mortality groups were scattered throughout the stand and thus tree spacing and size varied somewhat, but averaged roughly 10 cm DBH, 3.5 m tall, and 0.75 to 1 m apart.

Trees with no chlorotic needles, evidence of reduced leader growth, basal resinous, or mycelial fans and located several meters from each diseased group, served as controls. Control (51 total) and study trees (104 total) in the 17 disease centers were excavated with small hand tools (Shaw, 1980) to expose roots and buried materials. Resulting excavations were approximately 0.6 m wide, 0.9 m deep, and up to 6 m long. The light, uniformly textured soil derived from dacite volcanic pumice enabled excavation of residual degraded

wood, small roots, and rhizomorphs with minimal disturbance to root contacts, infection points (lesions) on roots, residual inoculum, and rhizomorphs.

The time of death for each study tree was determined for three proceeding years by examining the color and retention of needles; trees killed earlier were recorded as dead more than three years. The number and location of lesions on each root system and, where possible, the inoculum source for each infection was recorded. Each disease center was sketched to show healthy roots, infected roots, root lesions, root grafts, root contacts, and location of residual inoculum (Figures 3 and 4). Roots with mycelial fans beneath the bark were recorded as infected. Living roots without such fans or lesions were recorded as healthy. Isolations were made from randomly selected infected roots, but no cultures were obtainable from residual inoculum. All isolates recovered from infected roots were identified as *A. ostoyae* by the *in vitro* cultural methods of Morrison *et al.* (1985)—the fungus that caused the extensive damage in the former stand on this site (Shaw 1984).

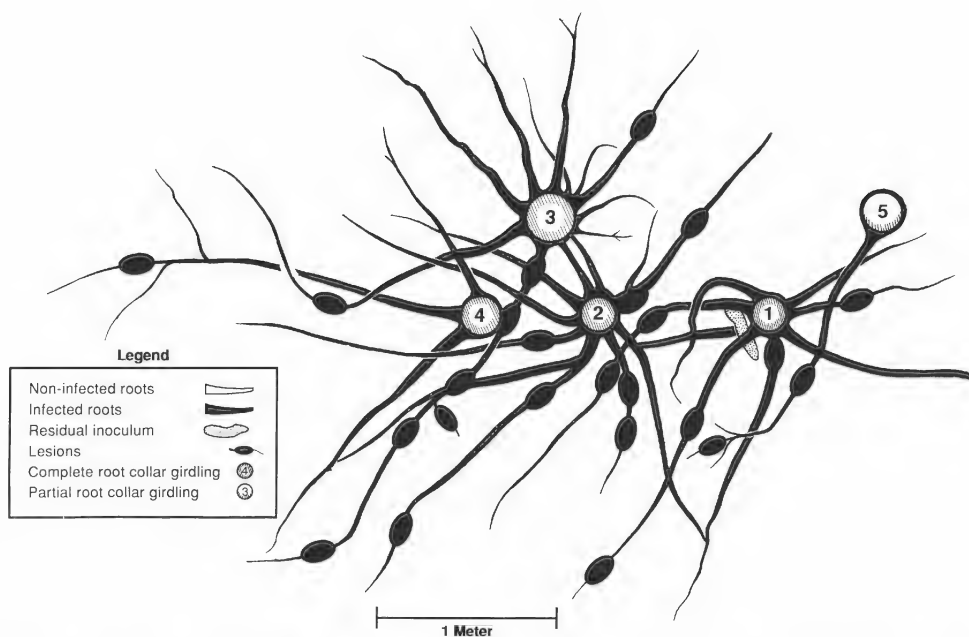


Figure 3. Schematic representation of a disease center (No. 15) showing rhizomorphs and numerous lesions on root systems. Increasing numbers represent the chronology of death.

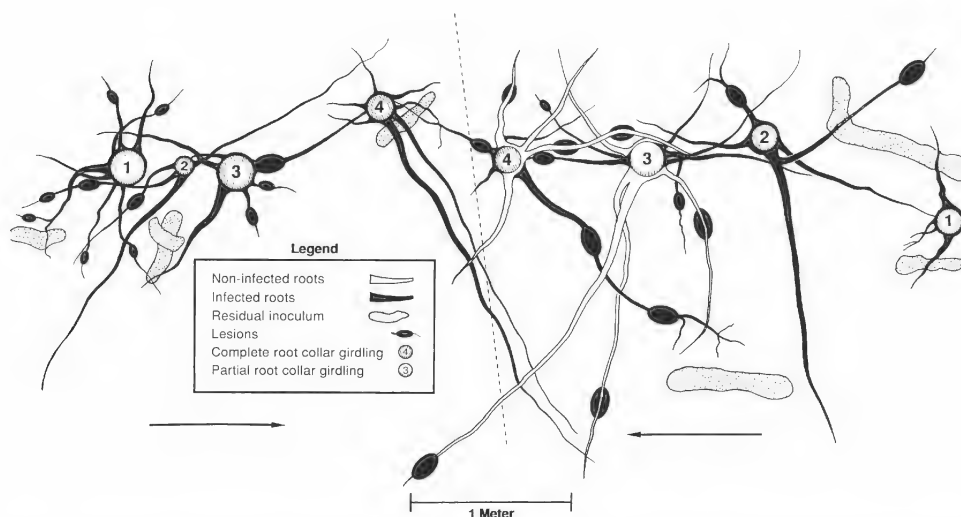


Figure 4. A schematic representation of two disease centers that may have coalesced to form one large center (No. 6). Probable direction of disease spread is denoted by arrows; the outer boundary of each "center" ends at the dotted line. Increasing numbers represent the presumed chronology of death in each center at one year intervals.

Results

The first trees to die in 15 of the 17 disease centers were infected via residual inoculum near or contacting the root collar (Figures 3 and 4). Other dead trees in these centers (Table 1), were infected and subsequently killed by contagion. In one instance, an infected root only 0.5 cm in diameter from a previously killed tree was grafted to the taproot of an adjacent tree, resulting in its infection. The chronosequence of tree death in disease centers No. 4 and No. 11 (Table 1) could not be determined; residual inoculum was not found and needles were absent from all dead trees—indicating that they died at least 3 years prior to our excavations.

TABLE 1. Distribution of infection by *Armillaria* on ponderosa pine roots by source—residual or secondary inoculum

Root Disease Center No. ^{a,b}	No. of Trees and (roots) ^c Examined	No. of Trees Infected From:	
		Residual	Secondary
1	4 (13)	1	3
2	10 (31)	3	7
3	6 (35)	2	4
4	3 (16)	0	3
5	8 (17)	2	6
6	8 (41)	2	5
7	3 (10)	1	2
8	8 (41)	1	7
9	3 (22)	1	2
10	7 (27)	2	5
11	6 (27)	2	6
12	12 (25)	4	8
13	7 (21)	3	4
14	3 (15)	1	3
15	6 (27)	2	4
16	5 (17)	1	4
17	5 (31)	2	3
Total	104 (400)	28	76

^aRoot disease centers were excavated in the summers of 1987 and 1988, 14 to 15 years after stand establishment.

^bThe original source of infection in root disease centers No.'s 4 and 11 could not be traced to residual inoculum (see text).

^cTotal number of primary roots examined on all trees in each center is in parentheses.

Residual material found near root collars of dying or recently killed trees ranged from small, deteriorated root fragments to intact pieces of wood that supported rhizomorphs to rare residual inoculum still containing the stringy, water-soaked wood

typical of advanced decay caused by *Armillaria*. No firm wood from the previous stand was unearthed nor did we strike any large, residual tap roots.

Nearly all residual inoculum found away from the root collars was badly deteriorated with no apparent *Armillaria* mycelial fans or rhizomorphs—it was usually distinctly gray in color, dry, and easily crumbled. This deteriorated inoculum was not associated with root collars or even roots of the present stand, suggesting that only a small portion of the residual inoculum functioned in perpetuating disease. These observations do not, however account for the probability that some fragments of this nature may have been previously functional and in contact with root collars of dead trees pulled between 1973 and 1983. The limited residual inoculum found in excavations around control trees was usually not in contact with roots or was only associated with their distal portions and not root collars.

In two instances, residual inoculum was responsible for infection of trees on opposite edges of reasonably large centers and roots of these trees intermingled with those from other trees in the center (Figure 4). Previously distinct, small centers appear to have coalesced by the time of our examination to form one larger center of now indistinguishable origin (Figure 4).

Rhizomorphs were rarely encountered “free” in the soil and never where they appeared to function as primary inoculum. They were found occasionally beneath the bark on functioning residual inoculum but more often they occurred epiphytically on infected and non-infected roots of the regeneration. When present on infected roots, rhizomorphs usually occurred at lesions and were embedded in the surrounding, resin-soaked soil.

Roots of *Armillaria*-killed trees had abundant lesions and invariably had mycelial fans extending beneath the bark, usually along the entire length of the root. Numerous lesions also were found on roots of control trees; however, all except one of these lesions were occluded and mycelial fans were absent on these roots. On the 372 roots from symptomatic trees, 163 lesions were found. Some roots had only one lesion, others had as many as 10, often in a “beadlike” arrangement along the root. Of the 395 roots examined on control trees, 46 lesions were found with a maximum of three on any one root.

Sampling was inadequate among various stand densities to determine how density might effect the epidemiological process we encountered; however, within the generally high range we studied, density appeared to have little effect on disease development.

Discussion

When treated in 1971, the study site was occupied by a disease-depleted stand of young-growth pine and a few, scattered, old-growth trees. We suspect that the various sanitation treatments left groups of extensively decayed tap roots of pole-sized trees more or less *in situ*. Stronger, medium-sized roots were largely removed from the soil by treatments which also may have scattered smaller, broken pieces of *Armillaria* infected roots somewhat uniformly across the site. It appears to be this latter material that is accountable for most subsequent disease centers and was encountered 16 years later in our excavations.

In unmanaged forest, early mortality of trees regenerating onto areas infested with *Armillaria* develops from infections on roots that are near or in contact with previously killed trees (Adams 1972, 1974; Wargo and Shaw 1985). As seedlings enlarge into trees, contacts among roots of neighboring trees arise, become more common, allow for tree-to-tree spread of the fungus, and lead to patch development of root disease (Shaw 1980). Damage may be confined to a few early losses, but it also can extend marked through subsequent tree-to-tree spread of the pathogen (Rykowski 1984, Wargo and Shaw 1985). Our data show that the dynamics of root disease development in managed stands on infested sites are similar to those in preceding natural stands, even where extensive inoculum removal operations have been conducted.

The development of underground signs and symptoms of fungal attack (i.e. lesions, rhizomorphs, mycelial fans, basal resinosis) on individual trees also appear to be analogous to that described for older natural stands in this area (Shaw 1980), including the occurrence of multiple lesions on a single root. These lesions likely developed as rhizomorphs grew epiphytically along roots and penetrated the cambium through openings in bark scales (Woeste 1956, Redfern 1978). This behavior and contacts with residual inoculum, which was largely exhausted by the time of our

study, and with diseased roots of other young trees may account for the many lesions we encountered on distal portions of root systems. In older trees, Shaw (1980) found distal spread of the fungus from such resinous lesions on live roots which resulted in the fungus residing as a perthophyte. Perhaps the lesions examined in this study were too young or the trees too small to express this condition.

This study demonstrated that the dynamics of infection on sites treated for root disease can change from primary, residual inoculum to contagion in the early stages of stand development, some 10 to 12 years after regeneration. Even small, infected roots on trees killed by contacting residual inoculum can act as secondary inoculum and spread *Armillaria* to other pines.

We assume that these expanding infection centers will continue to enlarge via contagion as the trees age—as they do in untreated, naturally regenerated stands (Shaw 1980, Shaw *et al.* 1976). If the extent of resulting damage is somewhat offset by the development of any possible resistance or tolerance to the fungus as the trees age (Morrison *et al.* 1992), remains to be seen. Relating eventual damage in treated stands to the effectiveness of inoculum reduction through sanitation (Roth and Shaw, unpublished) will be particularly important to managers contemplating initial control actions and in their determining if any follow-up treatments (Morrison *et al.* 1992) may be needed.

These data also can aid efforts to model the dynamics and impact of *Armillaria* root disease in forest stands (Shaw *et al.* 1991, Stage *et al.* 1990) by providing site specific data for equations that calculate the longevity and effectiveness of inoculum and “time to death” multipliers for infected trees (Stage *et al.* 1990). Such local adjustments to the Western Root Disease Model are necessary to increase the accuracy and utility of predictions for disease spread and impact that foresters must make during development of management plans.

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Literature Cited

- Adams, D. H. 1972. The relation of cover to the distribution of *Armillaria mellea* in a ponderosa pine forest. Oregon State University, Corvallis, Oregon, Ph.D. Dissertation.
- . 1974. Identification of clones of *Armillaria mellea* in young growth ponderosa pine. Northwest Science 48:21-28.
- Arnold, R. 1981. Nothing can stump this pulling machine. Western Conserv. J.:38-42.
- Bloomberg, W. J. and G. Reynolds. 1988. Equipment trials for uprooting root-rot-infected stumps. Western J. Appl. Forestry 3:80-82.
- Ecenbarger, W. 1992. The humongous fungus debate. Audubon 94:20-21.
- Hadfield, J. S., D. J. Goheen, G. M. Filip, C. R. Schmitt, and R. D. Harvey. 1986. Root diseases in Oregon and Washington conifers. U.S. Dep. of Agr., For. Serv. Pac. Northwest Reg., R6-FPM-250-86. 27 p.
- Hagle, S. K., and C. G. Shaw, III. 1991. Avoiding and reducing losses from Armillaria root disease. Chapter 11 in: Shaw, C. G., III; Kile, G. A. (eds.), Armillaria Root Disease. Agriculture Handbook No. 691. Washington, DC: U.S. Dep. of Agr., For. Serv. 246 p.
- Kile, G. A., G. I. McDonald, and J. W. Byler. 1991. Ecology and disease in natural forests. Chapter 8 in: Shaw, C. G., III; Kile, G. A. (eds.), Armillaria Root Disease. Agriculture Handbook No. 691. Washington, D.C.: U.S. Dep. of Agr., For. Serv. 246 p.
- Morrison, D. J., D. Chu, and A. L. S. Johnson. 1985. Species of *Armillaria* in British Columbia. Can. J. Plant Pathol. 7:242-246.
- Morrison, D. J., G. W. Wallis, and L. C. Weir. 1988. Control of Armillaria and Phellinus root diseases: 20-year results from the Skimikin stump removal experiment. Can. Forestry Serv., Pac. Forestry Res. Centre, Information Rep. BC-X-302. 16 p.
- Morrison, D., H. Merler, and D. Norris. 1992. Detection, recognition, and management of Armillaria and Phellinus root diseases in the southern interior of British Columbia. Forestry Can., Pac. Forestry Res. Centre FRDA Report #179. 25 p.
- Redfern, D. B. 1978. Infection by *Armillaria mellea* and some factors affecting host resistance and the severity of disease. Forestry 51:121-135.
- Redfern, D. B. and G. M. Filip. 1991. Inoculum and infection. Chapter 4 in: Shaw, C. G., III; Kile, G. A. (eds.) Armillaria Root Disease. Agriculture Handbook No. 691. Washington, D.C.: U.S. Dep. of Agr., For. Serv. 246 p.
- Rykowski, K. 1984. Niektóre troficzne unwarunkowania patogeniczności *Armillaria mellea* (Vahl) Quel. w uprawach sosnowych. [Some trophic factors in the pathogenicity of *Armillaria mellea* in Scots pine plantations]. Prace Instytutu Badawczego Lesnictwa 640:1-140.
- Shaw, C. G., III. 1980. Characteristic of *Armillaria mellea* on pine root systems in expanding centers of root rot. Northwest Sci. 54:137-144.
- . 1984. *In vitro* responses to gallic acid fail to distinguish between pathogenic and "non-pathogenic" species of *Armillaria*. p. 161-183 in: Kile, G. A. (ed.), Proceedings of the Sixth International Conference on Root and Butt Rots of Forest Trees; CSIRO, Melbourne. 430 p.
- Shaw, C. G., III, and L. F. Roth. 1976. Persistence and distribution of a clone of *Armillaria mellea* in a ponderosa pine forest. Phytopathology 66:1210-1213.
- Shaw, C. G., III, L. F. Roth, L. Rolph, and J. Hunt. 1976. Dynamics of pine and pathogen as they relate to damage in a forest attacked by *Armillaria*. Plant Dis. Rept. 60:214-218.
- Shaw, C. G., III, A. R. Stage, and P. McNamee. 1991. Modeling the dynamics, behavior, and impact of Armillaria root disease. Chapter 10 in: Shaw, C. G., III; Kile, G. A., (eds.), Armillaria root disease. Agriculture Handbook No. 691. Washington, D.C.: U.S. Dep. of Agr., For. Serv. 246 p.
- Stage, A. R., C. G. Shaw, III, M. A. Marsden, J. W. Byler, D. L. Renner, B. Eav., P. J. McNamee, G. A. Sutherland, and T. M. Webb. 1990. User's Manual for the Western Root Disease Model. Gen. Tech. Rep. Int. No. 267. Ogden, UT: U.S. Dep. of Agr. For. Serv., Intermountain For. and Range Exp. Sta. 32 p.
- Wargo, P. M., and C. G. Shaw, III. 1985. Armillaria root rot—The puzzle is being solved. Plant Dis. 69:826-832.
- Williams, R. E., C. G. Shaw, III, P. M. Wargo, and W. H. Sites. 1989. Armillaria root disease. For. Insect and Dis. Leaflet 78 (Rev.). U.S. Dep. of Agr., For. Serv. 8 p.
- Woeste, U. 1956. Antomische Untersuchungen über die Infektionswege einiger Wurzelpilze [Anatomical fungi]. Phytopathologische Zeitschrift 26:225-272. [Rev. of Appl. Mycol. 35:800].

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Effects of Human Disturbances on Prairies and the Regional Endemic *Aster curtus* in Western Washington

Abstract

The glacial outwash prairies of the Puget Trough have been used by humans for centuries, but the effects of recent human disturbances on them or their endemic plants have not been documented previously. The vegetation of prairies disturbed to varying degrees by off-road vehicles and by alteration of the pre-colonial fire regime was sampled using permanent plots. Indirect ordination and regression analysis show that increasing vehicular disturbance causes the diverse natural bunchgrass community to be replaced by a less diverse community dominated by exotic sod-forming grasses over a small suite of exotic forbs. The available evidence suggests that post-colonial disturbances have irreversibly deflected secondary succession in this community. Discriminant analysis predicts that *Aster curtus*, a regional endemic, would be present only where the cover of native bunchgrasses exceeds 32 percent. Thus with disturbance of the soil, *Aster curtus* and other native species are replaced, perhaps permanently, by weedy exotics.

Introduction

Coarse gravels deposited in the Puget Trough by retreating glaciers allowed prairies to develop roughly 10,000 years ago in a region where dense conifer forests typically dominate (Lang 1961, Ugolini and Schlichte 1973). Since their origin, these prairies have attracted people, who found them a ready source of food plants (Norton 1979). Food production was increased by frequent fires (Norton 1979), which also set back woody species that would otherwise have invaded (Lang 1961).

The term "prairie" was applied to these grasslands by European settlers in the mid-1800s and still occurs repeatedly on local maps. Many prairies are currently being used for pastures, gravel mines and home sites. Due to habitat destruction, the largest remaining prairies are located on Ft. Lewis, a U.S. Army base lying between Tacoma and Olympia, Washington. In addition, changes in the landscape (e.g. roads and plowed fields) apparently have reduced the pre-colonial fire frequency (Giles 1970), allowing for the invasion of the prairies by Douglas fir trees (*Pseudotsuga menziesii*; nomenclature throughout follows Hitchcock and Cronquist 1977).

Ft. Lewis encompasses the largest prairies in the Puget Trough, but the least disturbed example of this community type occurs on Rocky Prairie (M. Sheehan, pers. comm.). The original extent of Rocky Prairie has been greatly reduced by pastures, a gravel pit and a rural subdivision. How-

ever, a 14 ha section, isolated near the turn of the century, is now managed by the Washington Department of Natural Resources as a Natural Area Preserve. Although ecologists have conducted studies on both relatively natural (del Moral and Deardorf 1976) and disturbed (Jackson 1982) prairies, the differences between them have not been studied previously.

Most of the plants native to the Puget Trough prairies (e.g. *Festuca idahoensis*, *Solidago spathulata* and *Camassia quamash*) occur widely in western North America. However, *Aster curtus*, a small, perennial forb, is endemic to prairies of the Puget Trough and adjacent Willamette Valley. In Washington, *A. curtus* has rarely been found outside of glacial outwash prairies. It is on the list of sensitive taxa in Washington (Washington Natural Heritage Program 1987) and is a candidate for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1990).

The primary goal of this study was to describe and compare the vegetation of regional prairies that have been disturbed to varying degrees by humans. A secondary goal was to determine whether suitable habitat for *A. curtus* can be successfully identified from the abundance of other plant species.

Methods

Study Sites

This study was conducted on Rocky Prairie (46° 55' N, 122° 51' W) and on three of the largest grasslands on nearby Ft. Lewis: Weir Prairie (46° 54' N, 122° 43' W), 91st Division Prairie (47° 00' N, 122° 38' W), and 13th Division Prairie (47° 01' N, 122° 27' W). Some of the Ft. Lewis

¹Current address: Department of Conservation and Recreation, Division of Natural Heritage, 1500 E. Main St., Suite 312, Richmond, VA 23219

prairies have received little human use, but most show signs of disturbance, e.g. tire ruts and patches of bare soil. The center of the artillery range (91st Division Prairie) is heavily cratered and much of it burns annually, but it has been minimally disturbed by vehicles. The effects of these disturbances on the native prairies and the endemic *Aster curtus* have not previously been studied.

The prairies on Ft. Lewis are flat to rolling and often bordered by steep slopes. In contrast, Rocky Prairie features the unusual combination of mima mounds and larger swales and rises (Ritchie 1953). Both sites are underlain by Spanaway soils, which are rich in organic matter and nitrogen, but low in phosphorous, calcium, magnesium and potassium (R. B. Walker, pers. comm.). Grasses, primarily *Festuca idahoensis* and *Agrostis tenuis*, dominate both sites. Forbs such as *Hieracium cynosuroides*, *Camassia quamash* and *Lupinus* spp. are common. The low shrubs *Arctostaphylos uva-ursi* and *Symphoricarpos mollis* and Douglas fir trees occur in patches.

Field Sampling—Rocky Prairie

Four mima mounds were selected in a stratified random manner. On each of these, the vegetation was sampled using 41 0.25-m² quadrats: nine on the top and a set of four quadrats each on the sides and in the adjacent intermounds in each cardinal direction. The percent cover of each vascular plant species was noted in each quadrat in mid-May of 1983.

Field Sampling—Ft. Lewis

Historical use patterns of the Ft. Lewis prairies were determined from sets of aerial photographs taken between 1942 and 1981. Vehicle tracks and shell craters were the major disturbances visible in the photographs. These two disturbance types rarely co-occurred, and both apparently had declined since the 1960s. Other forms of disturbance were localized and are not considered here. Five disturbance classes were subjectively identified from the extent and intensity of vehicle tracks and shell craters: heavy (HV), moderate (MV), and light (LV) use by tracked vehicles, and heavy (HI) or light (LI) disturbance by artillery impacts.

Prairies representing four of the five classes were available for study (the heavily cratered center of the artillery range was inaccessible due to unexploded shells). Two circular plots (100 m²)

were established in areas representative of each disturbance class. In May 1984, the cover of all vascular plant species was recorded in 20 0.25-m² quadrats placed at 1 m intervals along the north/south and east/west axes of each plot.

Data Analysis

The mean vegetative cover, species richness and Shannon-Weiner diversity index (H' , Whittaker 1975) were calculated for each plot. Each species was identified as either native to the Pacific Northwest or an exotic (Hitchcock and Cronquist 1977). The relative proportion of native species and the relative proportion of the total cover they contributed were then calculated.

To evaluate the effects of human disturbances, the data from Ft. Lewis were analyzed using Detrended Correspondence Analysis (DCA) with the infrequently encountered species down-weighted (Hill 1979, Hill and Gauch 1980). A second ordination using the combined data from Ft. Lewis and Rocky Prairie was also conducted, but because of computational limits, data from the quadrats within each plot were pooled for this analysis. The patterns revealed in this ordination were investigated using linear regression, as performed by EPISTAT (Gustafson 1983).

To determine whether the presence of *Aster curtus* could be predicted from the abundance of other plants, data on the 40 most abundant plant species from Rocky Prairie were analyzed using Stepwise Discriminant Function Analysis (program BMDP7M of Dixon *et al.* 1981). The resulting classification function was checked by "predicting" which samples from Ft. Lewis would contain *A. curtus*.

Results

Diversity Measures

The prairies studied were sparsely vegetated; mean vascular plant cover exceed 100% in only one plot, and mean cover was less than 75% in four of the plots (Table 1). Among the 12 plots, species richness varied from 18 to 35, with higher values from Rocky Prairie. Up to 20 species were recorded in an individual quadrat, with the largest values from Ft. Lewis. Diversity (H') values ranged from 1.43 to 2.92, with the Rocky Prairie plots generally having the higher values.

TABLE 1. Descriptive statistics derived from the vegetation data for Ft. Lewis and Rocky Prairie. See text for definition of plot codes.

Plot Code	No. of Quadrats	Percent Cover	Species Richness		Diversity (H')
			Plot	Quad. Max. ^a	
LI-1	20	95	30	20	2.11
LI-2	20	74	32	16	1.92
LV-1	20	75	24	13	1.78
LV-2	20	92	28	19	2.00
MV-1	20	89	23	14	1.77
MV-2	20	71	25	16	2.37
HV-1	20	57	18	11	1.43
HV-2	20	79	21	11	1.48
RP-1	41	67	32	15	2.92
RP-2	41	82	35	17	2.44
RP-3	41	88	28	17	2.34
RP-4	33	102	31	16	2.01

^aMaximum number of species within a single 0.25 m² quadrat.

Ordination of the Vegetation Data

Most of the variation in the vegetation on Ft. Lewis occurred between, not within, plots (Figure 1). The

order of the eight plots determined by DCA closely matches my subjective appraisal of the degree of vehicular disturbance they had sustained, and they are arranged from least to most disturbed on the first axis (left to right in Figure 1). Quadrats from the most disturbed plots are intermixed at the right side of the diagram, indicating that these plots are floristically very similar to each other. They differ from the least disturbed plots by about 2.5 SD, indicating that vehicular disturbance has led to substantial changes in the species composition of these prairies.

The species ordination of the Ft. Lewis data (Figure 2) showed that the centers of distribution of most native species fell towards the left edge of the diagram, indicating the prominence of these species in the least disturbed plots. Exotic species and weedy natives tended to fall on the right side of the figure. Thus, as vehicular disturbance increases the native species are replaced by weedy ones, most of which are exotics. *Aster curtus* falls in the lower left corner, indicating that it has the greatest cover in the least disturbed prairies.

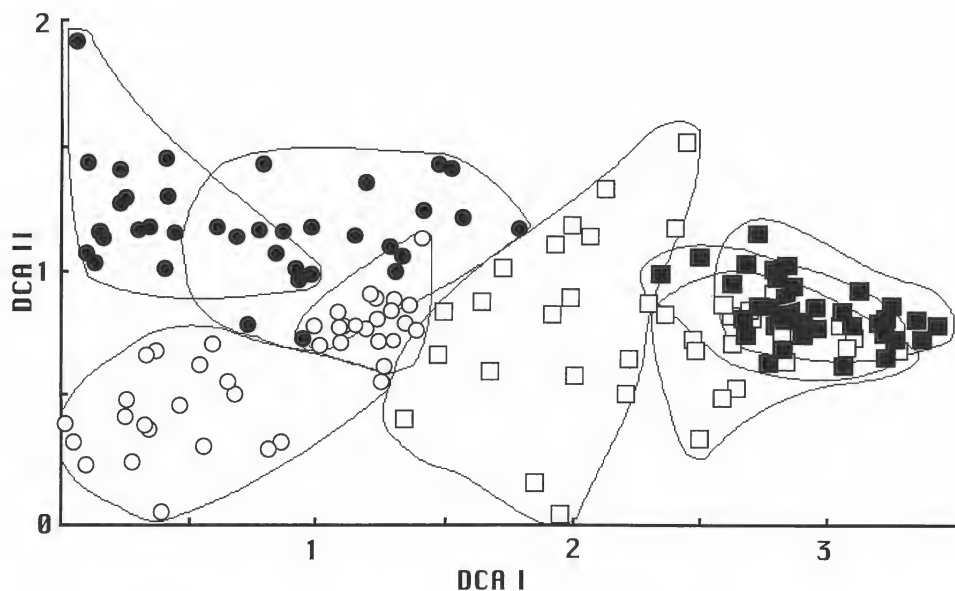


Figure 1. Scatter plot of DCA ordination of quadrat data from Ft. Lewis. The disturbance classes, abbreviations and symbols in the figure are: heavy vehicular, HV, solid square; moderate vehicular, MV, open square; light vehicular, LV, open circle; and light disturbance by artillery impacts, LI, solid circle. The 20 quadrats in each plot are outlined.

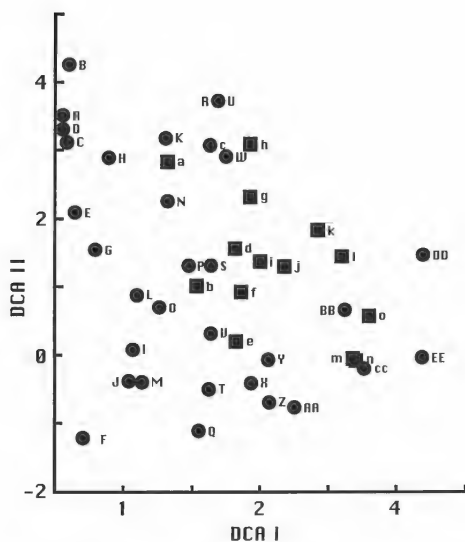


Figure 2. Scatter plot of DCA ordination of species from Ft. Lewis. Capitals represent native species, lower case letters represent exotics: A *Viola adunca*, B *Antennaria neglecta*, C *Sisyrinchium angustifolium*, D *Potentilla gracilis*, E *Solidago spathulata*, F *Aster curtus*, G *Hieracium cynoglossoides*, H *Ranunculus occidentalis*, I *Prunella vulgaris*, J *Microseris laciniata*, K *Dodecatheon hendersonii*, L *Eriophyllum lanatum*, M *Lomatium utriculatum*, N *Zigadenus venenosus*, O *Festuca idahoensis*, P *Lotus denticulatus*, Q *Camassia quamash*, R *Saxifraga integrifolia*, S *Luzula campestris*, T *Lupinus rivularis*, U *Juncus* sp., V *Pseudotsuga menziesii* seedlings, W *Frillaria lanceolata*, X *Danthonia californica*, Y *Carex pennsylvanica*, Z *Achillea millefolium*, AA *Fragaria virginiana*, BB *Veronica* sp., CC *Cerastium arvense*, DD *Arenaria* sp., EE *Galium* sp., a *Taraxacum officinale*, b *Rumex acetosella*, c *Trifolium dubium*, d *Aira caryophyllaea*, e *Hypericum perforatum*, f *Teesdalia nudicaulis*, g *Holcus lanatus*, h *Cytisus scoparius*, i *Hypochaeris radicata*, j *Anthoxanthum odoratum*, k *Chrysanthemum leucanthemum*, l *Plantago lanceolata*, m *Poa pratensis*, n *Trifolium pratensis*, o *Agrostis tenuis*.

The four plots from Rocky Prairie were clustered in the upper left corner of the ordination diagram for the pooled data (Figure 3). In other respects, the arrangement of plots closely resembled that in Figure 1.

The relative number and cover of native species declined along DCA axis I (Table 2). Similarly, while the relative cover of native bunchgrasses declined along this axis, the relative cover of exotic sod-grasses increased. Regression

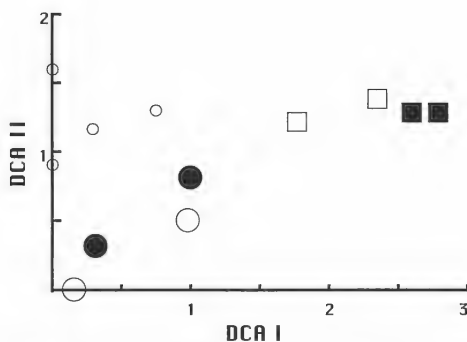


Figure 3. Scatter plot of DCA ordination of pooled plot data from Ft. Lewis and Rocky Prairie. Symbols are as in Figure 1, with the Rocky Prairie plots represented by small open circles.

TABLE 2. Descriptive statistics derived from the vegetation data for Ft. Lewis and Rocky Prairie. Plot codes as in Table 1.

DCA Axis I Score	Plot Code	Relative Richness: Native ^a	Relative Cover		
			Native ^a	Bunch ^b	Sod ^c
0	RP-4	77	98	47	1
1	RP-3	79	89	28	7
17	LI-1	73	88	46	2
27	LV-1	67	91	52	3
28	RP-2	71	79	37	16
73	RP-1	63	72	15	12
97	LV-2	54	63	42	8
97	LI-2	53	58	45	9
176	MV-2	48	38	11	25
241	MV-1	39	18	1	52
263	HV-2	38	6	1	62
278	HV-1	17	4	0	63

^aNative herbaceous species

^bPercent cover contributed by native bunchgrasses, primarily *Festuca idahoensis*.

^cPercent cover contributed by exotic sod grasses, primarily *Agrostis tenuis* and *Anthoxanthum odoratum*.

analysis showed that all of these trends were highly significant ($p < 0.001$).

Discriminant Analysis

Discriminant analysis correctly classified 72% of the quadrats from Rocky Prairie on the basis of the cover of *Festuca idahoensis* alone. The classification function derived at this step is

[1] $L = -2.118 + 0.066f$,

with f = the cover of *F. idahoensis* in the quadrat. Where $L > 0$, *Aster curtus* is predicted to be present; where $L < 0$, it is predicted to be absent. Setting $L=0$ and solving for f gives

$$[2] \quad f = 31.9.$$

Thus, *A. curtus* is predicted to be present where *F. idahoensis*, the community dominant in natural prairies, constitutes more than 32% cover, and absent when *F. idahoensis* is less abundant.

Stepwise addition of four more species (*Pteridium aquilinum*, *Lupinus rivularis*, *Anthoxanthum odoratum* and *Solidago spathulata*) increases the proportion of correctly identified samples to 80%. Of these, the first two are positive indicators while the other two indicate less-favorable habitat. Given both the small improvement in the function's predictive power and the ability of these species to grow, if not thrive, in weedy pastures, these species do not substantially improve the practical utility of the function.

Equation 1 correctly "predicts" whether or not *Aster curtus* would be present in 79% of the quadrats from the Ft. Lewis plots. This indicates that the equation is applicable to more than Rocky Prairie and supports the utility of *Festuca idahoensis* as an indicator of potential habitat for *A. curtus* in the Puget Trough.

Discussion

Vegetation Structure

The most species-rich quadrats were located in the least disturbed portions of Ft. Lewis, but the most species-rich plots were in Rocky Prairie. Unfortunately, differences in plot size and the number of quadrats sampled make it impossible to evaluate these differences in light of mid-scale topographic (mound to intermound) and microhabitat complexity. Studies of western Washington prairies by del Moral and Deardorf (1976) and Jackson (1982) reported that the cover, species richness, and composition of their study sites were similar to the moderately disturbed Ft. Lewis prairies sampled here. Studies of subalpine meadows in western Washington (e.g. Jackson 1982, del Moral 1985), which share many species with lowland prairies, have shown a range of richness values from lower than to substantially higher than those in Table 1. However, in contrast to their lowland counterparts, subalpine meadows typically support very few exotic species.

As disturbance increases the native bunchgrass, *Festuca idahoensis*, is replaced by a variety of sod-forming grasses, primarily *Agrostis tenuis*. The data in Table 2 and Figure 2 suggest that vehicular disturbance causes a loss of species, especially native ones. Since most of the forbs grow in the canopy gaps, forb species richness seems to be a function of canopy gaps and the availability of light near the soil surface.

As del Moral and Deardorf (1976) noted, mosses and lichens are abundant and diverse components of the native prairie flora. While I collected quantitative data only on the vascular plants, it is clear that the least-disturbed prairies I sampled also support a diverse non-vascular flora. As with the native vascular plants, the abundance and diversity of non-vascular plants apparently drops precipitously with vehicular disturbance. In heavily disturbed areas, mosses and lichens are rare and the soil surface is bare or covered with leaf litter.

In reviewing information on species-rich plant communities, R. Peet (unpubl.) has found that while tropical forests are species rich on a large scale, at a smaller scale the most species-rich communities are oligotrophic grasslands that are frequently burned or grazed. The results of the present study are consistent with this pattern. Indeed, the maximum values obtained here (ca. 20 species per 0.25 m²) are comparable with the maximum values that Peet has recorded from plots in northern Europe and the eastern United States. However, on a slightly larger scale (100 m²) the values reported in Table 1 are only one-half to one-third the maximum values that Peet has obtained. This may be a result of the relatively recent retreat of the glaciers from this region and/or the general decline in (regional) species richness with increasing latitude.

Jackson (1982) observed that Scatter Creek Prairie in western Washington is dominated by Eurasian grasses "despite more than 30 years with no grazing disturbance." Foin and Hektner (1986) found that post-grazing secondary succession in California coastal prairies has been deflected by the introduction of exotic, perennial grasses that exclude the native annual species. This indicates that both communities are brittle (*sensu* Westman 1978) and that grazing and other soil disturbances quickly push the community beyond its capacity to return to pre-disturbance composition. It is not clear, however, whether this change in composition

results primarily from the introduction of competitive exotic species, the removal of a keystone (Westman 1986) species or growth form, or from a shift in the biotic demands imposed on the constituent species (Mack and Thompson 1982). Further studies to address these questions would be worthwhile.

Identification of *Aster curtus* Habitat

Discriminant analysis of the data from Rocky Prairie and Ft. Lewis supports my observation that *Aster curtus* is most likely to be found in sites dominated by *Festuca idahoensis*. On much of Ft. Lewis, *F. idahoensis* has been replaced by exotics such as *Anthoxanthum odoratum*, *Agrostis tenuis* and *Poa pratensis*. This is congruent with the observation by Mack and Thompson (1982) that bunchgrasses, such as *F. idahoensis*, are generally less tolerant of grazing and other disturbances than are sod-forming species.

Like most of the native forbs in the regional prairies, *Aster curtus* is a community subordinate that grows in the gaps between clumps of *Festuca idahoensis*. The presence of these gaps may explain why *A. curtus* persists in natural prairies, but not in disturbed ones, even though seedlings of both *F. idahoensis* and *Agrostis tenuis* severely suppressed seedlings of *A. curtus* in a greenhouse competition experiment (Clampitt 1987). One explanation for this is the greater availability of light in the gaps, which could be crucial for the recruitment of *A. curtus* seedlings. Alternatively, the mosses that carpet the canopy gaps of natural regional prairies may provide a better seed bed or substrate for rhizome growth, e.g. by holding moisture longer than the gravelly soil.

Aster curtus is a long-lived perennial that devotes much of its resources to the production of new shoots and rhizomes and is able to tolerate

the occasionally harsh conditions of the natural prairies (Clampitt 1987). Because mature plants can tolerate natural stresses, *A. curtus* may persist in areas where seedlings are no longer able to establish. The absence of *A. curtus* from areas that have been heavily disturbed and are dominated by exotics indicates that the plant cannot persist indefinitely under these conditions.

No completely natural prairies exist in western Washington today. Although Rocky Prairie is currently protected from most physical disturbances, the pre-colonial fire regime has not been restored. The fire regime of the prairies at the margin of the Ft. Lewis artillery range appears to most closely resemble the situation before the arrival of Euro-Americans. *Aster curtus* is abundant only in the least disturbed areas. In moderately or heavily disturbed areas, *A. curtus* is found only in patches receiving the least disturbance. Under severe vehicular disturbance, *A. curtus* is eventually extirpated, along with many of the other native species.

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Literature Cited

- Clampitt, C. A. 1987. The reproductive biology of *Aster curtus* (Asteraceae), a Pacific Northwest endemic. *Amer. J. Bot.* 74:941-946.
- del Moral, R. 1985. Competitive effects on the structure of subalpine meadow communities. *Can. J. Bot.* 63:1444-1451.
- del Moral, R. and D. C. Deardorf. 1976. Vegetation of the Mima Mounds, Washington State. *Ecology* 57:520-530.
- Dixon, W. J., M. B. Brown, L. Engelman, J. W. Frane, M. A. Hill, R. I. Jennrich and J. D. Toporek. 1981. BMDP statistical software. Univ. of Calif. Press, Berkeley.
- Foin, T. C., and M. M. Hektner. 1986. Secondary succession and the fate of native species in a California coastal prairie community. *Madroño* 33:189-206.
- Giles, L. J. 1970. The ecology of the mounds of mima Prairie with special reference to Douglas fir invasion. M.S. Thesis, Dept. of Botany, Univ. of WA, Seattle.
- Gustafson, T. L. 1983. EPISTAT statistical package for the IBM Personal Computer. T. L. Gustafson. Round Rock, TX.
- Hill, M. O. 1979. DECORANA—A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell Univ. Ithaca, NY.

- Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: An improved ordination technique. *Vegetatio* 42: 47-58.
- Hitchcock, C. L. and A. Cronquist. 1977. *Flora of the Pacific northwest*. Univ. of WA Press. Seattle, WA.
- Jackson, L. E. 1982. Comparison of phenological patterns in prairie and subalpine meadow communities. *NW Sci.* 56:316-328.
- Lang, F. A. 1961. A study of vegetation change on the gravelly prairies of Pierce and Thurston Counties, western WA. M.S. Thesis, Dept. of Botany, Univ. of WA, Seattle.
- Mack, R. N. and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *Amer. Natur.* 119: 757-773.
- Norton, H. H. 1979. The association between anthropogenic prairies and important food plants in western Washington. *NW Anthro. Res. Notes.* 13: 175-200.
- Ritchie, A. M. 1953. The erosional origin of the mima mounds of southwest Washington. *Journal of Geology* 61: 45-50.
- Ugolini, F.C. and A.K. Schlichte. 1973. The effects of Holocene environmental changes on selected western Washington soils. *Soil Sci.* 116: 218-227.
- United States Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species. *Federal Register* 55:6184.
- Washington Natural Heritage Program. 1987. Endangered, threatened and sensitive vascular plants of Washington. WA Dept. of Natural Resources. Olympia, WA.
- Westman, W. E. 1978. Measuring the inertia and resilience of ecosystems. *BioScience* 28:705-710.
- . 1986. Implications of ecological theory for rare plant conservation in coastal sage scrub. pp. 135-140 in T. S. Elias, ed., *Conservation and Management of Rare and Endangered Plants*. The California Native Plant Society, Sacramento, CA.
- Whittaker, R. H. 1975. *Communities and Ecosystems*. Mac-Millan. New York.

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Feeding Ecology of Juvenile White Sturgeon (*Acipenser transmontanus*) in the Lower Columbia River

Abstract

The white sturgeon (*Acipenser transmontanus*) supports important recreational and commercial fisheries in the lower Columbia River. Little is known about the ecology of white sturgeon, and the feeding ecology in particular has received only limited investigation. From April through October 1988, the feeding ecology of juvenile white sturgeon was studied in two areas of the lower Columbia River. Overall, the tube-dwelling amphipod *Corophium salmonis* was the most important prey for the two size classes of juvenile white sturgeon studied. However, during all sampling periods and at both areas (River Kilometers [Rkm] 153 and 211), Size Class I white sturgeon (144-350 mm fork length) preyed more heavily on *C. salmonis* than did Size Class II white sturgeon (351 to 724 mm). Other temporally important prey for Size Class I white sturgeon included *Corophium spinicorne*, *Neomysis* sp., Chironomidae larvae, and eulachon (*Thaleichthys pacificus*) eggs; other temporally important prey for Size Class II white sturgeon included the bivalve *Corbicula fluminea*, *Corophium spinicorne*, Chironomidae larvae, and eulachon eggs. Index of Feeding analysis indicated that juvenile white sturgeon in both areas contained less food in September-October than in either May-June or July-August. Generally, the relationships between densities (abundances) of specific benthic organisms and white sturgeon diets were poor at Rkm 153 and 211. Despite the importance of *Corophium salmonis* in the diets of juvenile white sturgeon, it was not abundant in the benthos (mean density, <185 organisms/m² in April and September).

Introduction

The white sturgeon (*Acipenser transmontanus*), the largest North American sturgeon, is an anadromous species found along the west coast of North America from the Aleutian Islands, Alaska, to Monterey, California (Scott and Crossman 1973). Some populations in the Columbia River Basin are essentially landlocked due to dam construction (Cochner *et al.* 1985, Beamesderfer *et al.* 1990).

Historically, the population of white sturgeon in the Columbia River (Oregon and Washington) supported an intense commercial fishery, with catches peaking in 1892 at more than 2.4 million kg (Craig and Hacker 1940). However, due to overfishing, catches declined, and in 1899 the total catch was less than 33,250 kg. During the early 1900s, annual catches were less than 104,930 kg (Craig and Hacker 1940).

Since the early 1900s, white sturgeon populations in the Columbia River, particularly the one downstream from Bonneville Dam (the lowermost dam), recovered sufficiently to support important recreational and commercial fisheries. Presently, the lower Columbia River (from the mouth to Bonneville Dam) supports one of the largest populations of white sturgeon. In 1991, the estimated recreational and commercial harvests in the lower Columbia River were 22,700 and 3,800 fish, respectively (Washington Department of Fisheries

and Oregon Department of Fish and Wildlife 1992). Based on the number of recreational angler trips in 1991, the white sturgeon is second only to salmonid species as the most popular recreational fish in the lower Columbia River (Washington Department of Fisheries and Oregon Department of Fish and Wildlife 1992).

Little is known about the ecology of white sturgeon, and the feeding ecology of juveniles in particular has received only limited investigation. The diets of small juvenile white sturgeon (<800 mm total length) have been described in the Sacramento-San Joaquin River Basin, California (Schreiber 1962, Radtke 1966), and in the Columbia River and its estuary (Muir *et al.* 1988). However, most of the white sturgeon collected by Muir *et al.* (1988) were from the estuary; only a small number (N < 54) were collected upstream from the estuary over a 3-month period.

We examined the seasonal feeding characteristics of two size classes of juvenile white sturgeon (144-350 mm fork length and 351-724 mm fork length) in two areas of the lower Columbia River in 1988. We assessed both the importance of various prey eaten and the feeding intensity. Also, we examined the relationship between the feeding characteristics of juvenile white sturgeon and benthic invertebrate communities and the relationship between white sturgeon catches and benthic invertebrate abundance.

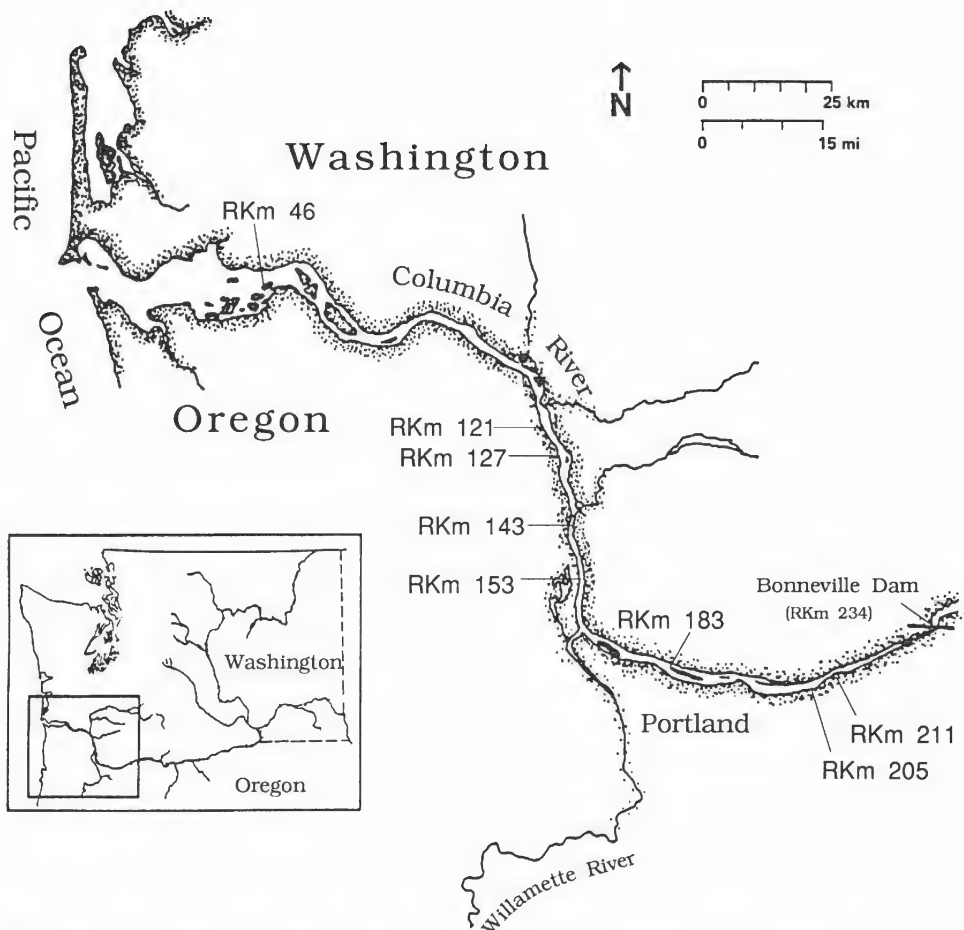


Figure 1. Map of the lower Columbia River showing the eight sampling areas where juvenile white sturgeon and benthic invertebrate samples were collected in 1988. Stomachs were collected from juvenile white sturgeon captured at River Kilometers (RKm) 153 and 211.

Methods

Juvenile white sturgeon were collected with a 7.9-m (headrope length) semiballoon shrimp trawl, which was towed by a 12.2-m boat, in eight areas of the lower Columbia River between River Kilometer (RKm) 46 and RKm 211 (Fig. 1). Mesh size in the trawl net was 38 mm (stretched measure) in the body; a 10-mm mesh liner was inserted in the cod end of the net. Trawling efforts were normally 5 min in duration in an upstream direction; boat speed varied depending upon water velocity, wind, and bottom topography. Distance traveled was es-

timated using a radar range-finder and used with the estimated fishing width of the net (5.3 m) to calculate the area fished. Sturgeon density for each effort was then calculated (number of sturgeon caught/area fished) and expressed as number/hectare (ha).

Trawling was done from late March through October. At each of the eight sampling areas, trawling was done along two or three parallel transects; one trawl was done along each transect. Transect 1 was closest to the Washington shore, Transect 2 was the middle transect, and Transect 3 was

closest to the Oregon shore. In river sections where only two transects were established, Transect 2 was closest to the Oregon shore.

All fishes captured in the trawl were identified and counted. Generally, all white sturgeon were measured (fork length to the nearest mm) and weighed (g). When a large number of white sturgeon was collected in a sampling effort, a subsample of at least 50 fish was measured and weighed.

Stomachs were taken from a subsample of white sturgeon captured at two areas (RKm 153 and 211; Fig. 1) to determine their diet and its relationship to the benthic invertebrate community. White sturgeon stomachs were taken during three time periods: (1) May-June, (2) July-August, and (3) September-October. At each area, we tried to obtain 25 stomachs from each of two size classes of white sturgeon during each sampling period. The two size classes were (I) 144 to 350 mm fork length and (II) 351 to 724 mm fork length. Stomachs were removed from the white sturgeon at capture, placed in individual vials containing a 7% buffered formaldehyde solution, and later transferred to vials containing 70% ethyl alcohol. Food items in each stomach were identified to the lowest practical taxonomic level, counted, and weighed (pooled by taxon) to the nearest 0.1 mg using a Mettler H-80 mechanical balance¹.

A condition factor, C (Everhart and Youngs 1981), was computed for each white sturgeon selected for stomach analysis using the formula

$$C = (W/L^3) \times 10^5,$$

where W = weight (g) and L = length (mm, fork length). Condition factors were compared between the three time periods for each size class using analysis of variance (ANOVA).

The diets of white sturgeon at RKm 153 and 211 were analyzed using two approaches. The relative contribution of a prey taxon to the diet was determined using a modification of the Index of Relative Importance (IRI) described by Pinkas *et al.* (1971)

$$IRI = (N + W) F,$$

where N = percent number of a prey item, W = percent weight of a prey item, and F = percent frequency of occurrence of a prey item. Index of Relative Importance values for individual prey items were then converted to percentages. To determine feeding intensity in each area, an Index

of Feeding (IF) was calculated using the equation

$$IF = (Ws \div Wf) \times 100\%,$$

where Ws = weight of stomach contents of a fish and Wf = weight of a fish. Differences among IF values were statistically tested using the Mann-Whitney test (Ryan *et al.* 1976).

Benthic macroinvertebrates were collected in April and September 1988 at two stations along each bottom trawling transect at the eight sampling areas (Fig. 1). Five benthic invertebrate samples were collected at each sampling station using a 0.1-m² Van Veen grab sampler (Word 1976). Each sample was sieved through a 0.5-mm screen and the residue preserved in a buffered formaldehyde solution (>4%) containing rose bengal. If it appeared that most of the material would not quickly wash through the sieve, the entire sample was preserved and sieved at the laboratory. The samples were later washed with water and preserved in a 90% alcohol solution. Benthic invertebrates were identified to the lowest practical taxonomic level and counted. Eulachon (*Thaleichthys pacificus*) eggs were also counted. When large numbers of eulachon eggs occurred in samples, their numbers were estimated by subsampling.

The relationships between white sturgeon densities (April and October) and *Corbicula fluminea* and *Corophium salmonis* densities (April and September) at the eight sampling areas were examined using simple and multiple regressions. Benthic invertebrate data collected in September were used to characterize the October period. White sturgeon densities were transformed to log₁₀ of (density + 1) and benthic invertebrate densities were transformed (log₁₀) prior to analysis.

Results

Stomach Contents

A total of 292 stomachs were taken from white sturgeon collected at RKm 153 and 211 in 1988. The amphipod *C. salmonis* was the most important prey item at both areas (Table 1). During all three time periods in both areas, percent Index of Relative Importance (%IRI) for *C. salmonis* was higher for the smaller Size Class I white sturgeon than for the larger Size Class II white sturgeon, indicating that the smaller juveniles preyed more heavily on *C. salmonis*. The importance of *C. salmonis* for Size Class I white sturgeon at RKm 153 remained

TABLE 1. Summary of white sturgeon diets from May through October 1988; numbers shown in the table are percents of total Index of Relative Importance (%IRI). Data are presented for two size classes—Size Class I (144-350 mm fork length) and Size Class II (351-724 mm fork length)—from two areas of the Columbia River, River Kilometers 153 and 211. Only prey items with %IRI values greater than 1 (for at least one size class and season) are shown.

Prey item	May-Jun		Jul-Aug		Sep-Oct	
	Size I	Size II	Size I	Size II	Size I	Size II
River Kilometer 153						
<i>Corbicula fluminea</i>	<1	11	<1	19	0	3
<i>Neomysis mercedis</i>	0	0	4	<1	<1	<1
<i>Corophium salmonis</i>	82	40	75	38	75	51
<i>Corophium spinicorne</i>	3	2	4	7	5	3
Heleidae larvae	<1	<1	3	3	<1	<1
Eulachon eggs	2	12	0	0	0	0
Digested material	11	34	13	32	21	41
River Kilometer 211						
<i>Corbicula fluminea</i>	<1	20	<1	35	<1	<1
<i>Neomysis</i> sp.	0	0	<1	0	20	2
<i>Neomysis mercedis</i>	0	0	<1	<1	<1	1
<i>Corophium salmonis</i>	59	12	75	24	44	24
<i>Corophium spinicorne</i>	<1	<1	1	<1	<1	<1
Hemiptera	0	0	0	<1	<1	1
Chironomidae larvae	0	<1	4	2	11	18
Chironomidae pupae	<1	0	0	<1	<1	4
Heleidae larvae	<1	<1	2	1	0	0
Eulachon eggs	25	51	0	0	0	0
Fish (unidentified)	0	3	0	0	0	0
Digested material	16	13	17	35	23	49

relatively consistent throughout the study, ranging from 75 to 82 %IRI during the three periods; whereas, at Rkm 211, the %IRI of *C. salmonis* was more varied, ranging from 44 (September-October) to 75 %IRI (July-August).

Size Class II white sturgeon also preyed primarily on *C. salmonis*, but, on occasion, they also consumed large quantities of the bivalve *Corbicula fluminea*, Chironomidae larvae, and eulachon eggs (Table 1). At Rkm 153, %IRI for *Corophium salmonis* ranged from 38% in July-August to 51% in September-October. Additionally, eulachon eggs (12 %IRI) and *Corbicula fluminea* (11 %IRI) were important prey in May-June, and *C. fluminea* (19 %IRI) and *Corophium spinicorne* (7 %IRI) were important in July-August. At Rkm 211, %IRI for *C. salmonis* ranged from 12% in May-June to 24% in July-October. Other important prey for this size class at Rkm 211 included eulachon eggs (51 %IRI) and *Corbicula fluminea* (20 %IRI) in May-June, *C. fluminea* (35 %IRI) in July-August, and Chironomidae larvae (18 %IRI) in September-October.

The IF analysis indicated a reduction in feeding of juvenile white sturgeon at Rkm 153 and 211 in September-October. At Rkm 153, IF values for both size classes of white sturgeon were significantly lower (Mann-Whitney test, $P < 0.05$) in September-October than in either May-June or July-August (Table 2). At Rkm 211, only Size Class II white sturgeon had significantly lower IF values in September-October than in May-June or July-August (Table 2). Besides lower IF values, the number of empty stomachs for both size classes in each area was highest in September-October, further indicating reduced feeding. There were no significant differences in C between the three time periods for either size class of white sturgeon (ANOVA, $P > 0.05$).

Water temperatures in areas where white sturgeon were collected for stomach analysis ranged from 13 to 18°C in May-June, 17 to 21°C in July-August, and 16 to 18°C in September-October.

TABLE 2. Comparisons of Index of Feeding (IF) for two size classes of juvenile white sturgeon collected at River Kilometers 153 and 211 in the Columbia River, 1988. Size Class I white sturgeon were 144-350 mm fork length and Size Class II white sturgeon were 351-724 mm fork length. Mean IF was calculated using only stomachs that contained food. The total number of stomachs collected and the number of empty stomachs are shown for each class.

Size Class	Time period		
	May-Jun	Jul-Aug	Sep-Oct
River Kilometer 153			
Size I			
a) mean IF	0.39	0.44	0.22 ^a
b) total number	26	24	20
c) number empty	0	0	3
Size II			
a) mean IF	0.27	0.35	0.08 ^a
b) total number	25	25	24
c) number empty	1	0	10
River Kilometer 211			
Size I			
a) mean IF	0.31	0.23	0.20
b) total number	27	25	24
c) number empty	2	0	6
Size II			
a) mean IF	0.38	0.41	0.03 ^a
b) total number	23	25	24
c) number empty	2	0	17

^aMean IF for Sep-Oct was significantly less than IF for both May-Jun and Jul-Aug; Mann-Whitney test, $P < 0.05$.

Benthic Invertebrates

Major benthic invertebrate taxa collected at Rkm 153 included Oligochaeta, *Corbicula fluminea*, *Corophium salmonis*, Chironomidae larvae, and Heleidae larvae (Table 3). At Rkm 211, major benthic invertebrate taxa included Turbellaria, Oligochaeta, *Corbicula fluminea*, Ostracoda, *Corophium salmonis*, Chironomidae larvae, and Heleidae larvae (Table 3). Eulachon eggs were included in the table because they were collected along with the benthic invertebrates and were important in the diet of white sturgeon. Densities of specific invertebrates often varied considerably among transects within each area.

Overall, the relationships between white sturgeon diets and specific benthic invertebrate densities were poor at Rkm 153 and 211 (Figs. 2 and 3). Although *C. salmonis* was by far the most im-

portant prey for both size classes of white sturgeon in May-June and September-October at Rkm 153, it was not an abundant benthic invertebrate (mean density, < 185 organisms/m² in both April and September). Eulachon eggs, which were abundant in the benthos at Rkm 153 during April, were an important food item for Size Class II white sturgeon during May-June. Heleidae larvae, although relatively abundant at Rkm 153, particularly during April, were insignificant in white sturgeon diets. Likewise, oligochaetes were relatively abundant at Rkm 153 during September, yet were not eaten by white sturgeon.

At Rkm 211, *C. salmonis* was by far the most important prey in both May-June and September-October for Size Class I white sturgeon; however, it was not abundant in the benthos in either April or September (mean density, < 120 organisms/m² in each month). *Corbicula fluminea* was the most abundant benthic invertebrate at Rkm 211 in April and was also an important prey for Size Class II white sturgeon in May-June. Eulachon eggs were abundant at Rkm 211 during April and were an important prey for both size classes of white sturgeon, particularly Size Class II fish, in May-June. In September, oligochaetes, *C. fluminea*, and Heleidae larvae were the most abundant benthic invertebrates at Rkm 211, yet these taxa were unimportant in the diet of white sturgeon in September-October.

The relationships between white sturgeon densities and densities of *Corbicula fluminea* and *Corophium salmonis* at the eight sampling areas (data combined for all areas) were poor (Table 4). Simple regression analysis indicated that overall (combining the data for April and September-October), only 7% of the variation in white sturgeon densities was explained by *Corbicula fluminea* densities; 20% of the variation was explained by *Corophium salmonis* densities. Multiple regression analysis showed that 28% of the variation in white sturgeon densities was explained by using both *Corbicula fluminea* and *Corophium salmonis* densities as predictors. The data were also analyzed separately for the two time periods. For April, 12% of the variation in white sturgeon densities was explained by *Corbicula fluminea* densities, and 11% of the variation was explained by *Corophium salmonis* densities. Multiple regression analysis indicated that 26% of the variation in white sturgeon densities in April was explained by using both *Corbicula fluminea* and *Corophium salmonis* densities

TABLE 3. Mean densities (number/m²) and standard deviations (SD) of major benthic taxa collected in April and September 1988 at River Kilometers (Rkm) 153 and 211 in the Columbia River. The total for each transect includes both major taxa and less important taxa not shown.

Rkm-transect	Taxon	April 1988		September 1988	
		Mean	SD	Mean	SD
153-1	Oligochaeta	405	444	1,849	697
	<i>Corbicula fluminea</i>	1,198	1,455	213	153
	Heleidae larvae	640	1,094	431	306
	Eulachon eggs	134,366	105,229	0	0
	Total	136,655	103,352	2,507	956
153-2	<i>Corbicula fluminea</i>	513	530	39	36
	Heleidae larvae	939	545	198	175
	Total	1,592	1,049	251	202
153-3	<i>Corbicula fluminea</i>	428	369	68	122
	<i>Corophium salmonis</i>	389	285	545	262
	Chironomidae larvae	78	90	0	0
	Heleidae larvae	146	156	8	15
	Total	1,144	798	625	377
	Entire area ^a	49,701	88,979	1,128	1,161
211-1	Oligochaeta	13	24	78	50
	<i>Corbicula fluminea</i>	1,210	860	478	370
	Heleidae larvae	772	509	500	284
	Eulachon eggs	8,874	14,262	0	0
	Total	10,930	14,028	1,110	558
211-2	Turbellaria	66	130	7	12
	<i>Corbicula fluminea</i>	544	908	248	253
	Heleidae larvae	301	467	440	386
	Total	982	1,212	739	582
211-3	Oligochaeta	406	214	627	645
	<i>Corbicula fluminea</i>	224	216	70	50
	Ostracoda	59	94	5	8
	<i>Corophium salmonis</i>	309	143	221	84
	Chironomidae larvae	43	49	52	53
	Eulachon eggs	55	49	0	0
	Total	1,135	325	1,016	810
	Entire area ^b	4,122	8,850	955	657

^a The average of all samples taken at Rkm 153; in April, only 28 samples were analyzed for the entire area.

^b The average of all samples taken at Rkm 211; in April, only 29 samples were analyzed for the entire area.

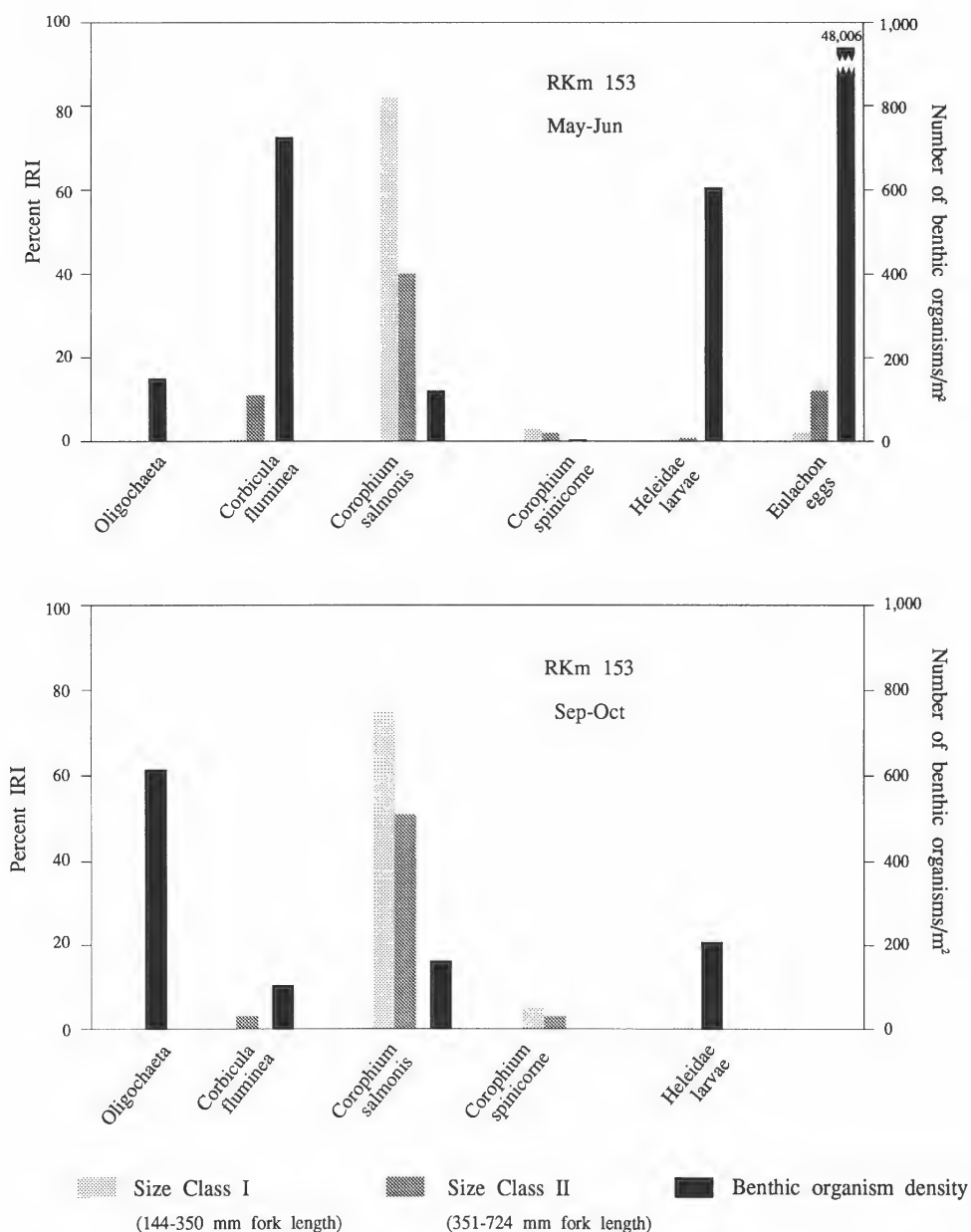


Figure 2. Percent Index of Relative Importance (%IRI) for prey of two size classes of juvenile white sturgeon collected during May-June and September-October 1988 at River Kilometer (RKm) 153 in the Columbia River. Also shown are densities of selected benthic organisms collected in April and September 1988; the April data are presented for the May-June period because no benthic sampling was done in May or June. Eulachon eggs are shown because they were collected along with the benthic invertebrates and were important white sturgeon prey.

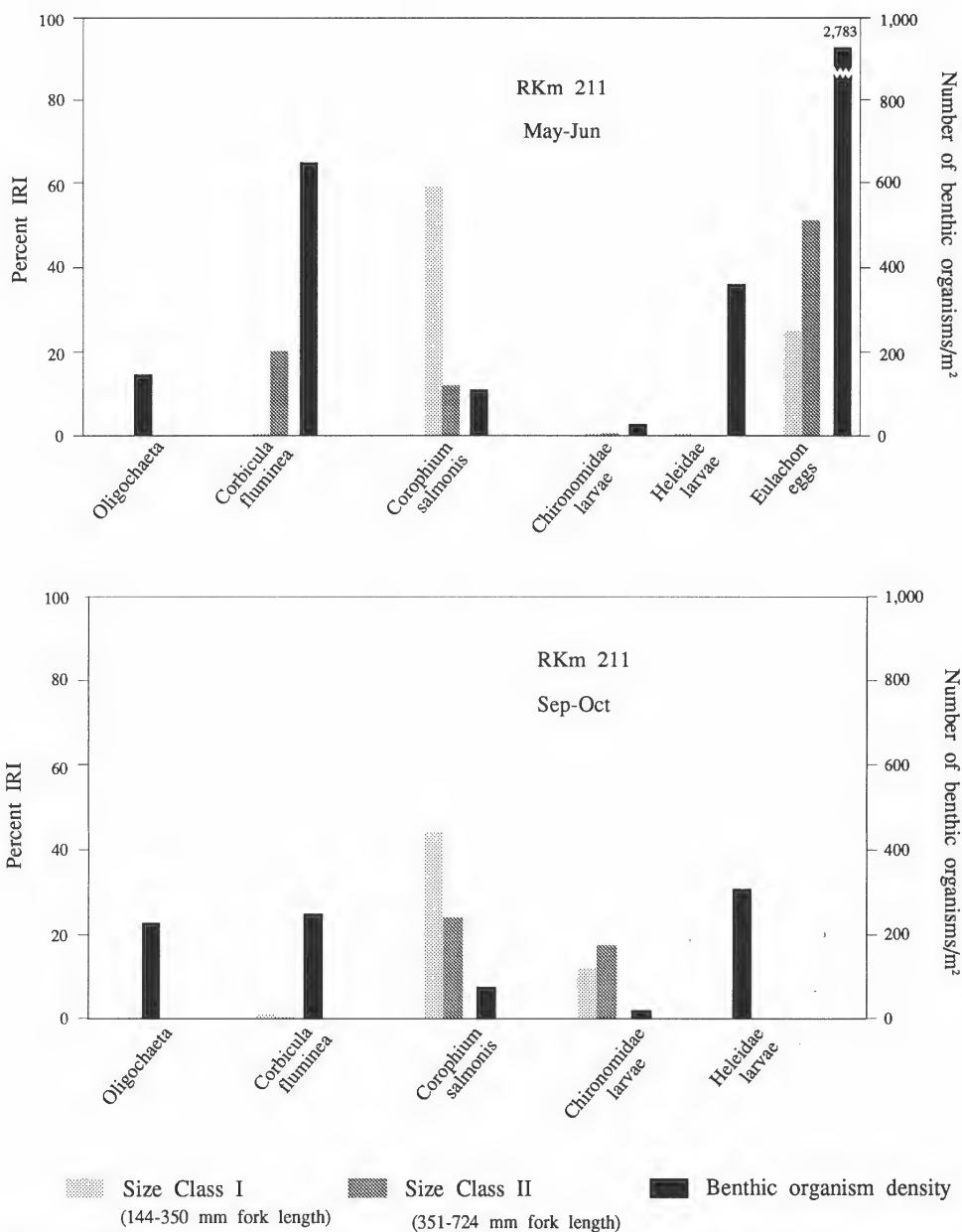


Figure 3. Percent Index of Relative Importance (%IRI) for prey of two size classes of juvenile white sturgeon collected during May-June and September-October 1988 at River Kilometer (RKm) 211 in the Columbia River. Also shown are densities of selected benthic organisms collected in April and September 1988; the April data are presented for the May-June period because no benthic sampling was done in May or June. Eulachon eggs are shown because they were collected along with the benthic invertebrates and were important white sturgeon prey.

TABLE 4. Summary of white sturgeon densities (number/ha) and benthic invertebrate densities (number/m²) at eight sampling areas (River Kilometer [RKm]-transect) in the lower Columbia River, 1988. Mean densities are shown for the invertebrates *Corbicula fluminea* (Cf) and *Corophium salmonis* (Cs), which are important prey for juvenile white sturgeon.

RKm-transect	Apr			Sep-Oct		
	Sturgeon density	Invertebrate		Sturgeon density	Invertebrate	
		Cf	Cs		Cf	Cs
46-1	0	29	55	0	171	604
46-2	6	88	6,574	0	103	1,516
46-3	24	563	1,046	0	234	4,567
121-1	0	3	5	12	594	20
121-2	0	115	86	0	365	68
127-1	251	4	2	51	536	49
127-2	48	108	6	74	67	16
127-3	8	351	75	6	357	316
143-1	0	177	231	0	212	17
143-2	23	219	3	10	461	5
153-1	561	1,198	2	334	213	4
153-2	—	513	29	18	39	5
153-3	—	428	389	3	68	545
183-1	0	201	1	0	292	18
183-2	0	176	9	8	661	68
205-2	0	42	33	2	56	6
205-3	54	572	12	7	686	3
211-1	78	1,210	26	198	478	9
211-2	531	544	5	763	248	8
211-3	0	224	309	0	70	221

^a Sturgeon were collected in October 1988.

^b Benthic invertebrates were collected in September 1988.

as predictors. For the September-October period, 3% and 32% of the variations in white sturgeon densities were explained by *Corbicula fluminea* and *Corophium salmonis* densities, respectively. Multiple regression analysis of the September-October data showed that 33% of the variation in white sturgeon densities was explained by using both *Corbicula fluminea* and *Corophium salmonis* densities as predictors.

Discussion

The feeding ecology of juvenile white sturgeon in our study, in general, agrees with findings from the lower Columbia River feeding study of Muir *et al.* (1988). Although fewer white sturgeon stomachs were analyzed for content during their study, they also found that the predominant prey

for white sturgeon less than 800 mm (total length) captured in the lower Columbia River and its estuary was *Corophium salmonis*. In Muir *et al.*'s (1988) study, neither *Corbicula fluminea* nor eulachon eggs were important prey for white sturgeon less than 800 mm long; this was in contrast to what we observed. Muir *et al.* (1988) sampled in the Columbia River only in July-September when eulachon eggs would not be present. This time period was well past the spawning migrations of eulachon.

Although RKm 153 and 211 are intensively used by juvenile white sturgeon, these areas do not have high standing crops of *C. salmonis*. In both areas, *C. salmonis* had mean densities less than 125/m² (average of all samples taken in each area) during April 1988. For comparison, the mean density of *C. salmonis* at four stations (RKm 30-40) in Cathlamet Bay, which is primarily a freshwater

bay in the Columbia River estuary, was 7,739/m² in April 1984 (Emmett *et al.* 1986). At RKm 46 (upper estuary), the mean density of *C. salmonis* was 2,420/m² in April 1988.

Considering the relatively low densities of *C. salmonis* in the benthos at RKm 153 and 211 and their importance in white sturgeon diets, it is possible that juvenile white sturgeon are (1) feeding on *C. salmonis* carried to them by the current drift, (2) moving to nearby areas with higher *C. salmonis* densities and feeding there, or (3) very efficiently feeding on *C. salmonis*, even when not abundant. *Corophium* spp. are often important river drift organisms and have been observed in white sturgeon egg and larval samples collected with plankton nets fished along the bottom at RKm 193 and 230 (Muir 1990). Davis (1978) observed that *C. salmonis* undergoes a vertical diel migration in the water column in the Columbia River estuary. *Corophium volutator*, a related Atlantic species, has also been found to swim above the bottom during part of its life cycle (Hughes 1988). If *C. salmonis* populations in freshwater sections of the lower Columbia River exhibit similar behavior, they could be dispersed by river currents. During the early part of the 1988 field season, we tried to sample invertebrate drift just above the bottom using an epibenthic sled; however, the sled would often fill with sand when towed along the bottom.

Juvenile white sturgeon may feed in shallow water, where *C. salmonis* is sometimes more abundant. In 1990, monthly mean densities of *C. salmonis* at individual stations in shallow water (1-6 m deep) at RKm 153 often exceeded 1,200 organisms/m², whereas monthly mean densities at the deeper water stations (11-21 m deep) generally were less than 105 organisms/m² (McCabe and Hinton 1991). However, at RKm 211, monthly mean densities of *C. salmonis* at the three shallow-water stations were low and usually did not exceed 76 organisms/m² (McCabe and Hinton 1991). The populations of *C. salmonis* found at the shallow-water stations at RKm 153 may represent a good food source for juvenile white sturgeon in the area. Although juvenile white sturgeon in the lower Columbia River typically favor deeper water (≥ 9.1 m) during daylight (McCabe and Hinton 1990), they may move into shallower water at night to feed. Studies using juvenile white sturgeon that have been tagged with sonic or radio tags are needed to describe their diel movements.

Juvenile white sturgeon may not be selectively preying on *Corophium salmonis* and *Corbicula*

fluminea. They may be preying primarily on *Corophium salmonis* and secondarily on *Corbicula fluminea* because these invertebrates are more available to them than other benthic invertebrates. *Corophium salmonis* is a tube-dwelling amphipod that migrates vertically in the water column in the Columbia River estuary (Davis 1978). This amphipod has also been observed crawling over the bottom in the Columbia River estuary (G. T. McCabe, Jr., personal observation). *Corbicula fluminea* is primarily a filter feeder (Way *et al.* 1990) with short siphons and apparently lives in close proximity to the substrate surface. Eulachon eggs, which were an important white sturgeon prey during May-June, are found attached to the substrate surface. Oligochaetes and Heleidae larvae may be found deeper in the substrate, and therefore be largely unavailable to juvenile white sturgeon.

Benthic invertebrate populations were not sampled monthly, and it is likely that some invertebrate densities were higher or lower in May-June than indicated by the April survey. Also, numbers of invertebrates in October may have differed from those during the September survey. However, based on benthic data collected monthly at RKm 153 and 211 in 1990 (McCabe and Hinton 1991), it is unlikely that *Corophium salmonis* densities at the deeper water stations (typically where white sturgeon are more abundant during daylight) ever reached moderate or high densities. McCabe and Hinton (1991) observed that densities of *C. salmonis* fluctuated from June through September but remained low; densities never exceeded 380 organisms/m² and were usually less than or equal to 101/m².

In conclusion, results from our study highlight the importance of benthic invertebrates, particularly *C. salmonis*, in the diets of juvenile white sturgeon in the lower Columbia River. Seasonal changes were observed in the diets of juvenile white sturgeon, with reduced feeding occurring in September-October. Despite the importance of benthic invertebrates in the diets of juveniles, the relationships between densities of specific benthic organisms and white sturgeon diets were generally poor.

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Notes

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

Literature Cited

- Beamesderfer, R. C., T. A. Rien, C. A. Foster, and A. L. Ashenfelter. 1990. Report A. In A. A. Nigro (ed.) Status and habitat requirements of white sturgeon populations in the Columbia River downstream from McNary Dam. Ann. Rep. to Bonneville Power Admin. (Project 86-50), Portland, Oregon. Pp. 6-37.
- Cochnauer, T. G., J. R. Lukens, and F. E. Partridge. 1985. Status of white sturgeon, *Acipenser transmontanus*, in Idaho. In F. P. Binkowski and S. I. Doroshov (eds.) North American sturgeons: biology and aquaculture potential. Dr W. Junk, Dordrecht, The Netherlands. Pp. 127-133.
- Craig, J. A., and R. L. Hacker. 1940. The history and development of the fisheries of the Columbia River. U.S. Dept. Interior, Bur. Fish., Bull. 32(49):133-216.
- Davis, J. S. 1978. Diel activity of benthic crustaceans in the Columbia River estuary. Oregon State University, Corvallis. M.S. Thesis.
- Emmett, R. L., G. T. McCabe, Jr., T. C. Coley, R. J. McConnell, and W. D. Muir. 1986. Benthic sampling in Cathlamet Bay, Oregon—1984. Natl. Mar. Fish. Serv., Final Rep. to U.S. Army Corps of Engineers (Contract DACW57-84-F-0348), Portland, Oregon. 11 p. plus appendices.
- Everhart, W. H., and W. D. Youngs. 1981. Principles of fishery science. Cornell University Press, Ithaca, New York. 349 p.
- Hughes, R. G. 1988. Dispersal by benthic invertebrates: the *in situ* swimming behaviour of the amphipod *Corophium volutator*. J. Mar. Biol. Assoc. United Kingdom 68:565-579.
- McCabe, G. T., Jr., and S. A. Hinton. 1990. Report D. In A. A. Nigro (ed.) Status and habitat requirements of white sturgeon populations in the Columbia River downstream from McNary Dam. Ann. Rep. to Bonneville Power Admin. (Project 86-50), Portland, Oregon. Pp. 149-191.
- . 1991. Report D. In A. A. Nigro (ed.) Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam. Ann. Rep. to Bonneville Power Admin. (Project 86-50), Portland, Oregon. Pp. 145-180.
- Muir, W. D. 1990. Macroinvertebrate drift abundance below Bonneville Dam and its relation to juvenile salmonid food habits. Portland State University, Portland, Oregon. M.S. Thesis. 40 p.
- Muir, W. D., R. L. Emmett, and R. J. McConnell. 1988. Diet of juvenile and subadult white sturgeon in the lower Columbia River and its estuary. California Fish and Game 74(1):49-54.
- Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. California Dept. Fish and Game, Fish Bull. 152, Sacramento. 105 p.
- Radtke, L. D. 1966. Distribution of smelt, juvenile sturgeon, and starry flounder in the Sacramento-San Joaquin Delta with observations on food of sturgeon. In J. L. Turner and D. W. Kelley (compilers) Ecological studies of the Sacramento-San Joaquin Delta. Part II, Fishes of the Delta. California Dept. Fish and Game, Fish Bull. 136. Pp. 115-129.
- Ryan, T. A., Jr., B. L. Joiner, and B. F. Ryan. 1976. Minitab student handbook. Duxbury Press, Belmont, California. 341 p.
- Schreiber, M. R. 1962. Observations on the food habits of juvenile white sturgeon. California Fish and Game 48(1):79-80.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Bd. Can. Bull. 184. 966 p.
- Washington Department of Fisheries and Oregon Department of Fish and Wildlife. 1992. Status report—Columbia River fish runs and fisheries, 1938-91. Olympia, Washington. 224 p.
- Way, C. M., D. J. Hornbach, C. A. Miller-Way, B. S. Payne, and A. C. Miller. 1990. Dynamics of filter feeding in *Corbicula fluminea* (Bivalvia: Corbiculidae). Can. J. Zool. 68(1):115-120.
- Word, J. Q. 1976. An evaluation of benthic invertebrate sampling devices for investigating feeding habits of fish. In C. A. Simenstad and S. J. Lipovsky (eds.) Fish food habits studies, 1st Pacific Northwest technical workshop. Washington Sea Grant WSG-WO 77-2, University of Washington, Seattle, Washington. Pp. 43-55.

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Small Mammal and Amphibian Communities and Habitat Associations in Red Alder Stands, Central Oregon Coast Range

Abstract

Although red alder dominates many sites in the Oregon Coast Range, mammal and amphibian communities in these stands have not been described. We documented community structure and riparian area associations for small mammals and amphibians in three red alder stands. We sampled habitat, amphibians, and small mammals from 0 to 150 m from streams in three 40- to 50-year-old red alder stands in the central Oregon Coast Range. We did not detect differences ($P > 0.12$) between streamside and upland sites in 25 of 28 habitat characteristics, nor in capture rates for one amphibian species and four mammal species. Capture rates for *Ensatina* salamanders (*Ensatina eschscholtzi*) were higher in upland than in streamside habitats. Roughskin newts (*Taricha granulosa*) were the most common amphibian and the small mammal community was dominated by deer mice (*Peromyscus maniculatus*), Trowbridge's shrews (*Sorex trowbridgii*), Pacific shrews (*S. pacificus*), and Virginia opossums (*Didelphis virginiana*). Capture rates for five species were associated ($r > 0.7$) with the abundance of woody debris and/or vegetation on the sites. Nine species captured along streamside and four species captured in uplands were not predicted by an existing wildlife habitat relationships model. Red alder stands should be considered important landscape components contributing to small mammal and amphibian diversity.

Introduction

Red alder (*Alnus rubra*) is a fast-growing, nitrogen-fixing tree that occupies over 1 million ha of the western United States (Tarrant *et al.* 1983). Alder has long been considered a weed species, but it is now receiving more attention as an economically valuable resource (DeBell *et al.* 1978). Although 3.7% of the timber harvest was composed of hardwoods in the 1980s, this will probably rise to 11.4% by the year 2000, mostly from red alder (Sessions 1989).

Despite the increasing economic importance and widespread occurrence of red alder in riparian and upland sites, only Gomez (1992) quantified small mammal or amphibian communities in the Oregon Coast Range. He found higher abundance of small mammals and amphibians in red alder than in old-growth Douglas-fir (*Pseudotsuga menziesii*) forests (Gomez 1992). The importance of streamside habitat for maintaining small mammal diversity and abundance in western coniferous forests has been described in southwest Oregon (Cross 1985), the Oregon Cascades (Anthony *et al.* 1987, Doyle 1990), and the central Oregon Coast Range (McComb *et al.* 1993, Gomez 1992). There is considerable geographic variation in responses of small mammals to riparian habitat (Raedeke 1988).

Managers need information on vertebrate use of streamside and upland habitats, including red alder stands, if they are to meet guidelines estab-

lished by the National Forest Management Act and the Oregon Forest Practices Act (OFPA). The OFPA protects riparian vegetation along fish-bearing streams for anadromous fish and to reduce non-point source pollution (Brazier and Brown 1973). The effects of OFPA regulations on terrestrial vertebrates are unknown. However, Brown (1985: appendix 8) indicated that 97 species of terrestrial vertebrates would breed in closed sapling-pole red alder stands (the most mature stand condition he reported for red alder) and 114 species use this stand condition for feeding. Slightly higher use was predicted for closed sapling-pole hardwood and shrubby wetland stands (102 breeding, 140 feeding). Although the accuracy of these predictions has not been assessed, managers are widely using this information to make decisions.

Our objectives were to: 1) compare habitat characteristics and abundance of small mammals and amphibians between streamside and upland sites in 40- to 50-year-old red alder stands in the central Oregon Coast Range, 2) examine habitat relationships of small mammals and amphibians in these stands, and 3) compare the species that we detected in these stands to those predicted in a habitat relationships model (Brown 1985).

Study Area and Methods

We selected three 40- to 50-year-old red alder stands adjacent to or including second-order



Figure 1. Location of study areas in the central Coast Range, Oregon.

streams in the central Coast Range of Oregon (Fig. 1). All stands contained one or more first-order streams. Streams adjacent to and within the stands were 0.2-4.0 m wide, and 0.2-2.0 m deep. These stands are typical of human-induced (20-30 ha), unmanaged Coast Range alder forests. The northern stand (Fig. 1) was about 10 km west of Nashville ($45^{\circ}50'$ lat., $124^{\circ}40'$ long.) resulting from secondary succession following abandonment of old fields. The other two stands, one about 15 km southwest of Alsea ($45^{\circ}40'$ lat., $124^{\circ}40'$ long.) and about 3 km east of Sumner ($43^{\circ}30'$ lat., $123^{\circ}10'$ long.) resulted from natural regeneration following harvest of Douglas-fir in the 1940-1950's. Although the overstory was domi-

nated by red alder (basal area = $26 \text{ m}^2/\text{ha}$), scattered residual Douglas-fir and western redcedar (*Thuja plicata*) (basal area = $5 \text{ m}^2/\text{ha}$) were present in the stands. The shrub layer was dominated by salmonberry (*Rubus spectabilis*) and thimbleberry (*Rubus parviflorus*). Herbaceous vegetation was mostly sword fern (*Polystichum munitum*) and grasses.

We sampled the Nashville and Alsea stands in 1988 and the Sumner stand in 1989. We established three 10×10 sampling grids ($135 \times 135 \text{ m}$) in each stand such that second-order streams were adjacent to or included within each grid (Fig. 2). Points within grids were 15 m apart, lines of points were parallel to the stream, and they extended 60-135 m up the slope. Grids were $>50 \text{ m}$ from edges of adjacent stands. We determined the structure and composition of the habitat at each point by measuring habitat characteristics from the grid point (distances or basal area) or in a 5-m radius circle around the point (plant coverages, densities, and log lengths/ 79 m^2 , Table 1). All foliage cover estimates were made prior to leaf fall.

We defined streamside habitat (74-142 sample points/stand) as $<10 \text{ m}$ of the high-water mark of any permanent stream, corresponding to the minimum OFPA buffer strip width for streams $\leq 4 \text{ m}$ wide. Also, we included the full floodplain as streamside habitat on sites where the floodplain extended $>10 \text{ m}$ from the stream (maximum = 35 m). Habitat $\geq 50 \text{ m}$ from streams was considered

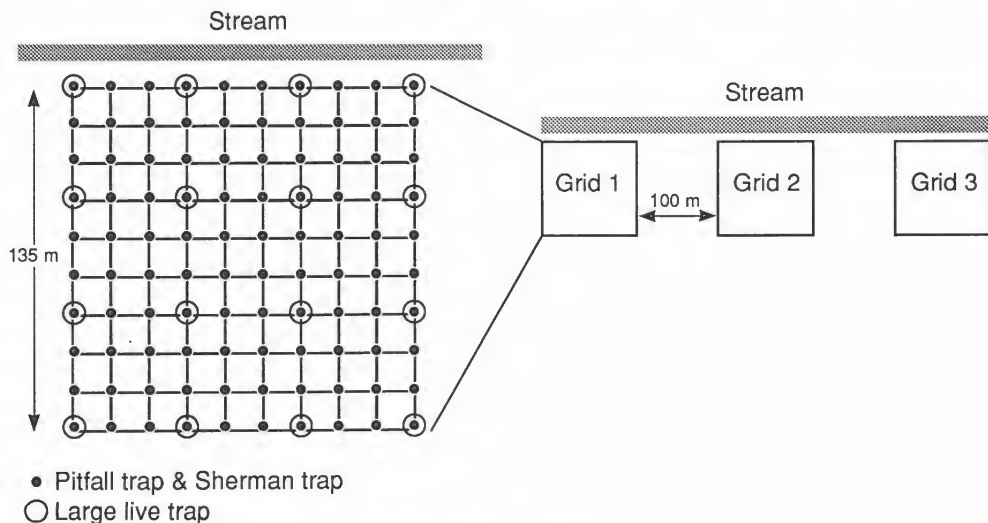


Figure 2. Schematic diagram of the sampling grid system used in the study.

TABLE 1. Average (SE) habitat characteristics among three habitat types in three red alder stands, Oregon Coast Range, 1988-89.

Characteristic	Streamside	Transition	Upland	P ¹
Distance to water (m)	5.9 (2.7)	32.1 (2.5)	71.2 (1.8)	0.0495
Slope (%) ²	41.5 (2.8)	43.7 (2.8)	48.8 (5.2)	0.2752
Rock cover (%) ³	2.0 (1.3)	0.2 (0.1)	0.3 (0.2)	0.1266
Slash cover (%) ³	1.7 (0.9)	1.0 (0.5)	1.5 (0.5)	0.8273
Litter depth (mm) ⁴	4.6 (1.0)	6.4 (2.0)	7.0 (1.9)	0.2752
Logs (m/79 m ²)				
10-19 cm diameter	16.5 (3.1)	16.5 (3.6)	15.9 (2.5)	0.8273
19-49 cm diameter	4.3 (1.7)	2.6 (0.9)	3.0 (1.0)	0.8273
50+ cm diameter	1.9 (1.0)	1.7 (0.9)	1.9 (1.1)	0.8273
Total	22.8 (4.9)	20.9 (5.0)	20.9 (3.6)	0.8273
Snags ⁵ /79 m ²	0.5 (0.1)	0.7 (0.2)	0.8 (0.2)	0.2752
Stumps ⁶ > 10 cm/79 m ²	0.8 (0.3)	0.9 (0.2)	1.1 (0.3)	0.2752
Basal area (m ² /ha)				
Deciduous	25.9 (1.2)	25.9 (0.7)	27.5 (3.9)	0.5127
Evergreen	3.2 (0.5)	4.9 (0.7)	8.2 (2.5)	0.1266
Total	29.1 (1.7)	30.8 (1.5)	35.7 (3.4)	0.0495
Woody plant cover (%) ³				
Deciduous 0-1 m tall	6.6 (0.7)	3.0 (0.5)	2.7 (0.2)	0.1904
Deciduous 1.1-5 m tall	22.8 (1.5)	13.6 (1.3)	21.9 (0.8)	0.9999
Deciduous > 5 m tall	54.0 (1.4)	51.7 (1.3)	56.1 (0.8)	0.9999
Evergreen 0-1 m tall	0.1 (0.1)	0.1 (0.1)	1.2 (0.2)	0.3537
Evergreen 1.1-5 m tall	0.1 (0.1)	1.2 (0.3)	1.2 (0.2)	0.5066
Evergreen > 5 m tall	2.8 (0.7)	3.9 (0.8)	7.0 (0.6)	0.3827
Tree density/79 m ²				
Deciduous 5-39 cm dbh	3.0 (0.8)	4.5 (0.3)	4.4 (0.2)	0.0495
Deciduous 40-79 cm dbh	0.4 (0.2)	0.3 (0.1)	0.4 (0.2)	0.8273
Deciduous > 80 cm dbh	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.3758
Evergreen 5-39 cm dbh	0.1 (0.1)	0.3 (0.1)	0.8 (0.3)	0.1266
Evergreen 40-79 cm dbh	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.2752
Evergreen > 80 cm dbh	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.2752
Fern cover (%) ³	23.2 (1.6)	33.4 (1.9)	36.7 (1.0)	0.1904
Forb cover (%) ³	13.8 (1.1)	9.2 (0.8)	4.9 (0.3)	0.0809
Grass cover (%) ³	3.3 (0.9)	3.1 (0.7)	1.6 (0.2)	0.6625

¹Comparing streamside with upland, Wilcoxon sign-rank test.²Measured with a clinometer 5 m upslope and downslope from plot center.³Ocular estimate of coverage.⁴Measured at 5 systematically arranged points within 5 m of plot center.⁵Dead stems > 5 cm dbh, > 2 m tall.⁶Dead stems > 5 cm dbh, < 2 m tall.

upland because McComb *et al.* (1993) found that capture rates for four small mammal species decreased dramatically beyond 50 m from streams in coniferous forests. All remaining habitat was considered transitional between streamside and upland.

We established one pitfall trap and one Sherman live trap within 2 m of each grid point. Pitfalls were number 10 tin cans, double deep, set flush with the surface of the ground along logs,

rocks, slope breaks or other natural drift fences where they were available (Corn and Bury 1990). To keep pitfalls free of water accumulation, we put drain holes in the cans and placed a metal cover approximately 10-15 cm above each pitfall. We tried to keep animals alive by supplying both Sherman traps and pitfalls with polyester bedding, hamster chow, peanut butter and rolled oats as bait. Sixteen regularly-spaced grid points on each sampling area had wire cage traps (20 x 20 x 90 cm,

Tomahawk) for sampling larger mammals. These traps were covered with polyethylene plastic for protection from rain and they were baited with sardines. Traps were set for eight consecutive nights in the early fall 23 August to 20 September, prior to most rains) and late fall (3-22 November, during consistent rains). All three sampling grids per stand were sampled simultaneously. Stands were sampled consecutively. Although capture rates for some species varied between sampling seasons, the distribution of captures among habitat types did not differ between seasons in this study, McComb *et al.* (1993), or (except for 3 small mammal species) Gomez (1992).

Animals that were captured alive were either ear-tagged or toe-clipped and released at the point of capture. Both living and dead animals were identified to species and the location of capture was recorded.

Statistical Analyses

Habitat characteristics and capture rates of species with >20 initial captures (recaptures were not considered) were compared between streamside and upland habitats with a Wilcoxon sign-rank test ($n=3$ stands). Stands were considered independent observations for these analyses. Populations were not estimated using standard mark-recapture methods because sampling grids were divided into habitat types for most analyses and because mortality of insectivores was too high (>30%).

We assessed habitat associations for species with >20 capture locations (8 species). We used Pearson product moment correlation to examine associations between captures per sampling grid and average habitat characteristics per sampling grid ($n=9$). These habitat analyses should be considered exploratory because grids within stands were probably more dependent on one another than were grids among stands. Hence, there is the potential for results to be confounded by stand effects.

Results and Discussion

Habitat characteristics

We were unable to detect differences between streamside and upland habitat in 25 of 28 characteristics (not including distance to water, Table 1). Deciduous trees 5-39 cm dbh were less abundant and total tree basal area was lower in streamside

than upland habitats (Table 1). Cover by forbs was higher along streamsides than in uplands. There was a trend toward greater rock cover, evergreen basal area, and density of 5- to 39-cm dbh evergreens in streamside than in upland habitat ($P=0.13$).

Animal Abundance

Amphibians. We captured 228 amphibians (8 species) and 10 reptiles (1 species) during 14,400 pit-fall trap-nights. Roughskin newts (*Taricha granulosa*) were the most common amphibian in both streamside and upland habitats. We could not detect differences between streamside and upland habitats in the relative abundance of roughskin newts (Table 2). However, capture rates for *Ensatina* salamanders (*Ensatina eschscholtzi*) were higher in upland than in streamside habitat (Table 2). McComb *et al.* (1993) and Gomez (1992) also found *Ensatina* salamanders more strongly associated with upland than riparian habitat in Coast Range conifer forests. Although some amphibian species require free water for reproduction, total amphibian captures were not associated with streamside habitat in these red alder stands. Average capture rates of Pacific giant salamanders (*Dicamptodon tenebrosus*, 0.9-1.9/1,000 trapnights [TN]) and *Ensatina* salamanders (1.5-6.4/1,000 TN) were similar to rates reported by Corn and Bury (1991) in unmanaged Douglas-fir forests (0.4-0.5 and 4.5-5.1/1,000 TN, respectively). Gomez (1992) did not find differences between red alder-dominated and conifer-dominated stands in the relative abundance of Pacific giant salamanders or *Ensatina*s. However, roughskin newt capture rates were higher on our sites (6.5-7.2/1,000 TN) than in unmanaged Douglas-fir forests (0.3-1.1/1,000 TN, Corn and Bury 1991). Gomez (1992) also captured more roughskin newts in red alder than in seral Douglas-fir stands. Western redback salamander (*Plethodon vehiculum*) capture rates were lower on our sites (0.7-2.2/1,000 TN) than in Douglas-fir forests (4.9-8.1/1,000 TN, Corn and Bury 1991). Gomez (1992) captured more redback salamanders in red alder than in pole-stage Douglas-fir stands. Corn and Bury (1991) considered northwestern salamanders (*Ambystoma gracile*) rare in Douglas-fir forests, but they were as abundant as Pacific giant salamanders on our sites (Table 2) and on Gomez's (1992) sites.

Dunn's salamanders (*Plethodon dunni*) were found to be streamside associates by both Gomez

TABLE 2. Average (SE) mammal and amphibian captures/1,000 trap nights among three habitat types in three red alder stands, central Oregon Coast Range, August–November 1988, 1989.

Species	Trap Type ¹	n	Streamside	Transition	Upland	P ²
Amphibians						
Roughskin newt	P	98	6.7 (4.4)	6.5 (3.9)	7.2 (5.5)	0.2752
Ensatina salamander	P	50	1.5 (0.4)	2.6 (1.8)	6.4 (2.9)	0.0459
western redback salamander	P	21	2.2 (1.5)	1.2 (0.8)	0.7 (0.4)	0.2752
Red-legged frog	P	19	2.1 (1.5)	1.2 (0.8)	0.7 (0.4)	
Pacific giant salamander	P	18	0.9 (0.7)	0.9 (0.5)	1.9 (1.5)	
northwestern salamander	P	13	0.9 (0.9)	1.4 (1.1)	1.3 (0.7)	
Other species ³		9	0.4 (0.2)	0.5 (0.5)	0.3 (0.3)	
Total	P	228	15.1 (2.4)	14.6 (2.5)	18.1 (2.8)	0.4298
Mammals						
Deer mouse	S	562	36.0 (3.3)	33.5 (2.7)	39.5 (7.8)	0.5127
Trowbridge's shrew	P,S	263	9.1 (1.0)	9.5 (1.7)	9.8 (0.6)	0.5127
Pacific shrew	P,S	89	4.2 (1.7)	2.2 (0.9)	3.1 (1.4)	0.5127
Townsend's chipmunk	S	45	1.6 (0.6)	4.3 (1.4)	3.4 (1.8)	0.5127
Oregon vole	P,S	25	0.8 (0.6)	0.9 (0.3)	0.9 (0.9)	0.8166
Northern flying squirrel	T,S	14	0.0 (0.0)	0.2 (0.2)	2.4 (2.4)	
Virginia opossum	T	11	8.5 (4.1)	3.1 (1.3)	3.5 (1.8)	
Other species ³		79	2.6 (0.7)	1.7 (0.4)	1.9 (0.8)	
Total		1088	36.0 (0.7)	33.4 (5.3)	38.7 (5.3)	0.5127

¹Pitfall (P) trapnights=14,400; Sherman (S) trapnights=14,400; Tomahawk (T) trapnights=2,304. Captures/1000 trapnights are based on trapnights/trap type.

²Wilcoxon sign-rank test.

³Reptiles and amphibians with <10 captures along streamside (S), upland (U), or both (B): tailed frog (U), Dunn's salamander (S), and common garter snake (S).

⁴Mammals with <10 captures along streamside (S), upslope (U), or both (B): Mountain beaver (*Aplodontia rufa*, S), California red-backed vole (B), long-tailed vole (S), Townsend's vole (S), ermine (B), house mouse (*Mus musculus*, S), dusky-footed woodrat (*Neotoma cinereus*, B), shrew-mole (B), red tree vole (U), raccoon (*Procyon lotor*, S), black rat (*Rattus rattus*, S), Coast mole (U), Townsend's mole (S), marsh shrew (B), western spotted skunk (S), eastern cottontail (*Sylvilagus floridanus*, U), and Douglas squirrel (*Tamiasciurus douglasii*, B).

(1992) and McComb *et al.* (1993). Gomez (1992) also identified tailed frogs (*Ascaphus truei*), red-legged frogs (*Rana aurora*), Pacific giant salamander, and roughskin newts as streamside associates in the Oregon Coast Range.

Mammals. We captured 1,088 mammals (24 species) in 31,104 trap-nights (all three trap types). The mammal community was dominated by deer mice (*Peromyscus maniculatus*), Trowbridge's shrews (*Sorex trowbridgii*), Pacific shrews (*S. pacificus*), and Virginia opossums (*Didelphis virginiana*). We did not detect differences between streamside and upland habitats in the capture rates of four species with >20 captures, nor did total small mammal captures differ between streamside and upland habitats (Table 2). Capture rates of Pacific shrews (2.2-4.2/1,000 TN) and Trowbridge's shrews (9.5-9.8/1,000 TN) were lower in the red alder stands that we sampled than in conifer stands

(2.5-6.0 and 13.5-19.1/1,000 TN, respectively, Corn and Bury 1991). Gomez (1992) did not detect differences between red alder and conifer stands in the relative abundance of Pacific shrews, but he found shrew-moles (*Neurotrichus gibbsii*) and Trowbridge's shrews more abundant in red alder than in Douglas-fir stands.

The affinity of various species for streamside habitat seems to vary geographically and from one plant community to another. Cross (1985) reported higher abundances of deer mice, Pacific shrews, shrew-moles, and Pacific jumping mice in streamside zones than in upland or transition zones in southwest Oregon. Doyle (1990) reported higher relative abundance in streamside than upland habitat for five of ten small-mammal species trapped on fourth- and fifth-order streams in the western Cascades, including 4 species found on our study sites: Trowbridge's shrew, deer mouse, Oregon vole

(*Microtus oregoni*), and ermine (*Mustela erminea*) (Doyle 1990). Doyle (1990) also found more California red-backed voles and Townsend's chipmunks (*Tamias townsendii*) in upland than riparian habitats. McComb *et al.* (1993) found no difference in total small mammal captures between upland and streamside habitats in coniferous forests. However, both McComb *et al.* (1993) and Gomez (1992) reported higher capture rates along streamside for Pacific jumping mice (*Zapus trinotatus*), marsh shrews (*Sorex benderii*), long-tailed voles (*Microtus longicaudus*), and white-footed voles (*Phenacomys albipes*) and higher capture rates in upland habitats for California red-backed voles (*Clethrionomys californicus*). Gomez (1992) also found Pacific shrews and Townsend's voles (*M. townsendii*) associated with streamside in the central Oregon Coast Range. Streamside habitat in the McComb *et al.* (1993) study was dominated by red alder and uplands were dominated by Douglas-fir, so some of these species may have been responding more to differences in tree communities than to proximity to free water.

There are at least three reasons why we were unable to detect differences between streamside and uplands habitats in capture rates for small mammals in our study. First, mammal community structure between streamside and upland habitats may be largely a function of differences in habitat structure and composition (Doyle 1990, McComb *et al.*, 1993). In our study, upland and streamside habitats were similar in structure and composition, and the capture rates of the common small mammals was similar between the two habitats as well. Second, McComb *et al.* (1993) found that although capture rates for marsh shrews, shrewmoles, deer mice and Pacific jumping mice declined beyond 50 m from the stream, capture rates for California red-backed voles and Trowbridge's shrews did not increase until > 200 m from a permanent stream in coniferous Coast Range forests. Thus, the upland red alder habitat that we sampled may have been too close to water to affect capture rates of some species. Finally, our sample sizes were small ($n=3$), so the power of our tests was low.

Habitat Relationships

The capture rates of five species were associated ($r > 0.7$, $P < 0.05$) with ≥ 1 habitat feature. Capture rates of roughskin newts and Oregon voles

were positively associated with the length of logs > 19 cm in diameter ($r > 0.70$) and with the number stumps ($r > 0.78$), while Pacific shrew capture rates were negatively associated with these features ($r = -0.71$, logs; $r = -0.77$, stumps). Further, roughskin newt capture rates were associated with evergreen shrub cover ($r = 0.84$) and deciduous tree basal area ($r = -0.71$). Capture rates for Townsend's chipmunks were associated with deciduous shrub cover ($r = 0.87$) and fern cover ($r = -0.76$), and capture rates for Trowbridge's shrews were associated with grass and forb cover ($r = -0.88$). The habitat relationships for small mammals are generally consistent with observations made by Maser *et al.* (1981), but several (log associations with Oregon voles, evergreen shrubs with roughskin newts) were opposite of associations detected by Gomez (1992) among red alder and Douglas-fir stands. Roughskin newts that we captured were probably migratory individuals that sought cover during their movements.

Comparisons with a Wildlife Habitat Relationships Model

These data gave us the opportunity to test Brown's (1985) predictions of species occurrence in red alder stands. Two major types of errors exist with a wildlife habitat relationships model: 1) the species was found using a habitat type but use was not predicted by the model, 2) the species was not found using the habitat type but use was predicted by the model. Of these errors, the first type can be detected with the greatest confidence. The second type of error is more difficult to detect because the sampling strategy may be inappropriate for certain species, insufficient stands may have been sampled, or if the species was rare, it may have been missed by chance. More subtle errors occur in designation of habitat types as primary (a preferred or optimal habitat necessary for long-term population maintenance) vs. secondary (used by a species, but less suitable than primary habitat) (Brown 1985). Further, Brown (1985) designated habitats as secondary where data were insufficient to clearly identify it as primary.

Streamside Pole Stands.—Our streamside samples were most similar to the closed sapling-pole stand condition of the hardwood and shrubby wetland plant community described by Brown (1985). We caught 6 of 10 reptile and amphibian species and 12 of 20 mammal species that were predicted

by Brown (1985) to use this habitat type for feeding, resting or breeding in this geographic region (within constraints of the sampling techniques). Western spotted skunks (*Spilogale gracilis*) were captured at two of the three sites and should be considered species that use streamside pole stands at least as secondary habitat. Six other species each were captured in only one stand: northwestern salamander, common garter snake (*Thamnophis sirtalis*), California red-backed vole, long-tailed vole, Townsend's mole (*Scapanus townsendii*), and coast mole (*Scapanus orarius*). Streamside pole stands may provide some habitat for these species, but these species should not be considered typical users of this habitat type.

Brown (1985) characterized closed-sapling pole riparian hardwood stands as being secondary habitat for western redback salamanders, deer mice, Trowbridge's shrews, Pacific shrews, and Townsend's chipmunks. These species were abundant in the streamside habitat that we sampled and they were consistently captured at all stands. Riparian hardwood closed-sapling pole stands probably should be considered primary habitat for these species.

Upland Pole Stands. Our upland samples were most similar to the closed sapling-pole stand condition of the red alder plant community described by Brown (1985). We caught 6 of 10 reptile and amphibian species and 13 of 17 mammal species that were predicted to use this habitat type for feeding, resting or breeding in this geographic region. California red-backed voles were captured at two of the three sites, so these stands may represent secondary habitat for this species. Tailed frogs, red tree voles (*Phenacomys longicaudus*), and Townsend's moles were each captured in only one stand. Upland pole stands may provide some habitat for these species, but they should not be considered typical users of this habitat type.

Brown (1985) characterized these upland pole stands as being secondary habitat for western redback salamanders, deer mice, Pacific shrews, Virginia opossums, and Townsend's chipmunks. These species were abundant in the upland habitat that we sampled and they were consistently captured at all stands. Red alder closed-canopy pole stands probably should be considered primary habitat for these species.

Management Implications

Oregon Forest Practices Act guidelines state that a riparian management area (RMA) shall be main-

tained on all fish-bearing streams. Its width is to average three times the stream width but it must not be < 7.6 m, and need not be > 30.3 m wide. Following harvest adjacent to the RMA, all pre-harvest logs, some live conifers, 50% of the pre-harvest shade level, and 75% of the shade over the aquatic zone must be retained. However, federal land management agencies sometimes maintain wider (30-50 m) RMA's to meet other needs, such as snag requirements. Timber harvest, usually clearcutting, may occur outside of RMA's. If RMA's extend > 10 m on each side of the stream and maintain a strip of preharvest habitat for small mammals and amphibians, then most of the species that we sampled might find at least marginal habitat in RMA's prior to harvest of adjacent upland areas. We will be assessing the influence of harvesting adjacent upland areas on these species in the future. If any of these species are adversely affected by induced edges (sensu Temple 1986), then narrow RMA's may not even provide marginal habitat for such species.

The stands that we studied were probably more heterogeneous than stands managed for red alder timber production. The heterogeneity among our sampling grids allowed us to assess the potential value to five species of including certain structural features within alder stands. For example, if upland red alder stands are harvested and regenerated with red alder, then retaining logs > 19 cm in diameter may provide cover for migrating rough-skin newts and resident Oregon voles. Brown (1985) identified > 150 species of vertebrates in western Oregon and Washington that use logs, so benefits of log retention or recruitment extend beyond these two species. Large logs would be unlikely to occur or persist in these alder stands unless conifers (especially Douglas-fir and western redcedar) are at least a minor component of the stand. Douglas-firs were a minor component of the naturally regenerated stands that we studied, but they were probably responsible for providing at least marginal habitat for red tree voles and California red-backed voles. We encourage land managers to consider managing alder stands that contain a minor component of Douglas-fir or western redcedar if enhancing vertebrate species richness is a goal.

Providing logs or conifers in small (~ 0.5 -ha) patches could reduce interference with harvesting operations and intermediate treatments. Conifers grown in these patches would add compositional

complexity and log recruitment to the stand. Capture rates of several species were associated with cover of either deciduous shrubs, primarily salmonberry and thimbleberry (also shrew-moles and Pacific jumping mice, Gomez 1992), or evergreen shrubs, predominantly salal (*Gaultheria shal-lon*), Oregon-grape (*Berberis* sp.), and huckleberry (*Vaccinium* sp.) (also tailed frogs and California red-backed voles, Gomez 1992). Hence, some effort should be made during site preparation and vegetation management to maintain a mixture of these species during stand development. Most of the deciduous shrubs in these stands reproduce vegetatively, so they may resprout after fire or mechanical site preparation. Patches of huckleberry and Oregon-grape may need some protection from site preparation to ensure their dominance in the developing stands. These recommendations represent hypotheses that should be tested by land managers.

Literature Cited

- Anthony, R. G., E. D. Forsman, G. A. Green, G. Witmer, and S. K. Nelson. 1987. Small mammal populations in riparian zones of different aged coniferous forests. *Murrelet* 68:94-102.
- Brazier, J. R. and G. W. Brown. 1973. Buffer strips for stream temperature control. For. Res. Lab., Oreg. State Univ. Res. Pap. 15. Oregon State Univ., Corvallis, Oregon. 9 p.
- Brown, E. R., ed. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. USDA For. Serv. Publ. No. R6-F&WL-192-1985. Pacific Northwest Region, Portland, Oregon. 2 volumes 634 p.
- Corn, P. S., and R. B. Bury. 1990. Sampling methods for terrestrial amphibians and reptiles. USDA For. Serv. Gen. Tech. Rep. GTR-PNW-256. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. 34 p.
- Cross, S. P. 1985. Responses of small mammals to forest riparian perturbations, in *Proc. Conf. on Riparian ecosystems and their management*. USDA For. Serv. Gen. Tech. Rep. RM-120. Rocky Mtn. For. Range Exp. Sta., Fort Collins, Colorado. Pp. 269-275.
- DeBell, D. S., R. F. Strand, and D. L. Reukema. 1978. Short-rotation production of red-alder: some options for future management, in *Utilization and management of alder*. USDA For. Serv. Gen. Tech. Rep. PNW-70. Pacific Northwest For. Range Exp. Sta., Portland, Oregon. Pp. 231-244.

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- Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. *J. Mammal.* 71:14-23.
- Gomez, D. G. 1992. Small mammal and herpetofauna abundance in riparian and upslope areas of five forest conditions. M.S. Thesis, Oregon State Univ., Corvallis. 118 p.
- Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981. Natural history of Oregon Coast mammals. USDA For. Serv. Tech. Rep. PNW-133. Pacific Northwest For. Range Exp. Sta., Portland, Oregon. 496 p.
- McComb, W. C., K. McGarigal, and R. G. Anthony. 1993. Small mammal and amphibian abundance in stream-side and upslope habitats of mature Douglas-fir stands, western Oregon. *Northwest Sci.* 67:7-15.
- Raedeke, K. (ed.) 1988. Streamside management: riparian wildlife and forestry interactions. Univ. of Washington, Instit. For. Resour. Contrib. No. 59. Univ. of Washington, Seattle. 277 p.
- Sessions, J., (coordin). 1989. Timber for Oregon's tomorrow: the 1989 update. For. Res. Lab., Oregon State Univ. Corvallis, Oregon. 183 p.
- Tarrant, R. F., B. T. Bormann, D. S. DeBell, and W. A. Atkinson. 1983. Managing red alder in the Douglas-fir region: some possibilities. *J. For.* 81:787-792.
- Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: comparison of two models, in J. Verner, M. L. Morrison, and C. J. Ralph, (eds.) *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates*. Univ. of Wisconsin Press, Madison. Pp. 301-304.

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Jin Zhen-hao, Li Heli, and Wang Shou-cai, Langxiang Forest Bureau, Heilongjiang Province,
People's Republic of China

Comparison of Small Mammal Populations and Diversity in Northeast China and Northwest Canada

Abstract

This study was designed to compare small mammal populations and diversity in similar cutover forest habitats in northeast China (Langxiang, Heilongjiang Province) and northwest Canada (Prince George, British Columbia). Populations were sampled on replicate live-trap grids during a period of high numbers of small mammals in autumn at each of the respective study areas. The brown-backed vole (*Clethrionomys rufocanus*) in China and the meadow vole (*Microtus pennsylvanicus*) in Canada dominated their respective communities with Jolly-Seber population estimates ranging from 59 to 104 voles/ha. Secondary major species included the northern red-backed vole (*C. rutilus*), Japanese field mouse (*Apodemus speciosus*), and striped field mouse (*A. agrarius*) in China, and the boreal red-backed vole (*C. gapperi*) and deer mouse (*Peromyscus maniculatus*) in Canada. Total average numbers of individuals were quite similar in each of the China (207) and Canada (209.5) communities. A greater biomass of small mammal species occurred at Langxiang (5.3 kg) than Prince George (4.2 kg) due to significantly larger body weights of *C. rufocanus* and *A. speciosus* than *M. pennsylvanicus* and *P. maniculatus*, respectively. Diversity measurements were similar, but species richness was somewhat higher in the small mammal community at Prince George than Langxiang. There was generally a remarkable similarity in relative abundance and diversity of small mammal species occupying young cutover forest lands in northeast China and northwest Canada. This similarity suggests that the principles of managing temperate forests for wildlife diversity in North America could be applied to similar forests in Asia.

Introduction

Forest habitats associated with early successional stages after timber harvesting are frequently dominated by herbaceous and deciduous shrub species. These habitats are highly desirable for various small mammal species since plant product (e.g. seed, fruits, vegetative parts) and invertebrate food sources are readily available. Small mammal communities on cutover forest land in temperate areas of North America are composed of mice (*Peromyscus* spp.), voles (*Microtus* spp. and *Clethrionomys* spp.), chipmunks (*Tamias* spp.), shrews (*Sorex* spp. and *Blarina* spp.), and several less common species (Gashwiler 1970, Hooven 1973, Hooven and Black 1976, Martell and Radvanyi 1977, Martell 1983, D'Anieri *et al.* 1987, Sullivan 1990).

In contrast, there is little information on small mammal communities in similar post-harvest forest habitats in temperate areas of Asia. Temperate forest management in northeast China (Heilongjiang Province, People's Republic of China) has resulted in some reports involving population outbreaks of the brown-backed vole (*C. rufocanus*) and other rodents (Hsia 1958, 1966,

Shu *et al.* 1975, Shu 1985). However, no detailed studies of small mammal communities in young forest habitats have been conducted. In general, knowledge of forest-wildlife relationships is poorly known or non-existent in Asia. Comparative studies of wildlife communities in temperate forests of Asia and North America could provide some direction in terms of both conceptual and management objectives.

This study was designed to compare small mammal populations and diversity in similar forest habitats in northeast China and northwest Canada. This comparison was conducted in similar early successional habitats after forest harvesting and during a period of high populations of small mammals at each of the respective study areas.

Materials and Methods

Description of study areas

The study area representing northwest Canada was located in the "wet cool central" (SBS_{wk}) subzone of the Sub-boreal Spruce (SBS) Biogeoclimatic Zone (Meidinger and Pojar 1991). Replicate study blocks (54°16' N, 122°14' W) were located

54 km northeast of Prince George, British Columbia, Canada. The climate is Dfc (Köppen) with cool summers and moisture all year. Characteristic forests in this area are composed of white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta* var. *latifolia*), with some subalpine fir (*Abies lasiocarpa*). Several deciduous species are common throughout: willow (*Salix* spp.), aspen (*Populus tremuloides*), black cottonwood (*P. trichocarpa*), paper birch (*Betula papyrifera*), and Sitka alder (*Alnus sinuata*).

Two replicate blocks were chosen at this study area. Block A (60.9 ha) was clearcut logged in the winter of 1976-77, broadcast burned in fall of 1977, and planted with white spruce in 1978. The terrain was essentially flat at an elevation of 750 m. Block B (56.2 ha) was located approximately 1.5 km from A. The original forest stand was clearcut logged in 1978, broadcast burned in 1979, and planted with white spruce in 1980. This area had a slight northwest aspect at 800 m elevation.

The study area representing northeast China was located in mixed coniferous and deciduous broad-leaved forest (Richardson 1990) at NanGou Forest Farm, 15 km southeast of Langxiang (46°56'45" N, 128°53'30" W), Heilongjiang Province. The climate is Dwa (Köppen) with hot summers and cold dry winters (Burger and Zhao 1988). The characteristic forest is composed of Korean pine (*Pinus koraiensis*) (up to 50% of stand volume mixed with valuable tolerant hardwoods such as *Tilia amurensis*, *Betula costata*, *Fraxinus mandshurica*, *Ulmus japonica*, *Acer mono*, *Juglans mandshurica*, and *Phellodendron amurense*); pioneer species are *B. platyphylla* and *Populus davidiana* (Burger and Zhao 1988, Richardson 1990). Boreal species such as *Larix gmelini*, *Abies nephrolepis*, *Picea jezoensis*, and *Picea koraiensis* occur at higher elevations (>900 m).

Two replicate blocks were also chosen at this study area. Blocks A and B were clearcut logged in 1979 and planted with Korean pine in 1981. These compartments were 7 and 6 ha, respectively, but were contiguous with a large mosaic (>100 ha) of similar-aged plantations on cutover forest land. As was the case at the Canadian study area, competition from herb and shrub species was considerable in these plantations. These vegetative conditions provided excellent habitat for small mammals.

Small mammal populations

Sampling of small mammal populations was done on four occasions at weekly intervals from 28 September to 22 October 1986 in China, and on four occasions at 3-week intervals from 27 August to 30 October 1987 in Canada. The shorter sampling interval in China reflected the limited amount of time available for the study. On each of the replicate blocks at each study area, a 1-ha checkerboard live-trapping grid with 49 (7 x 7) stations set at 14.29-m intervals was operated with two Longworth live-traps per station. Traps were baited with whole oats (mixture of corn, soy beans, and sunflower seed in China) and a slice of carrot (potato in China), and coarse brown cotton was supplied as bedding. Traps were set on day 1, checked on the morning and afternoon of day 2, and morning of day 3, and then locked open between trapping periods.

All small mammals (except shrews and weasels (*Mustela* spp.)) captured were ear-tagged with fingerling fish tags, sexed, reproductive condition noted by palpation of male testes and mammarys of the females, and weighed on Pesola spring balances. All animals were released at the point of capture immediately after processing. There was a high mortality rate for shrews because of the overnight trapping technique. Thus, shrews were collected for subsequent species identification and measurement of weight.

Complete enumeration using minimum number of animals known to be alive (MNA) (Krebs 1966) provided density values for each of the four trapping periods at each study area. Population densities were also estimated by the Jolly-Seber model (Seber 1982) for reasons indicated by Jolly and Dickson (1983). The average MNA value for the last three trapping periods and the average Jolly-Seber estimates for the second and third trapping periods were calculated for the major species on each grid. Values for the first trapping period were eliminated since this sample acted as a pre-baiting period at both study areas. Jolly-Seber does not estimate population parameters for the last sample period.

Species richness and diversity

Measurements of species richness and diversity were based on the number of individuals in each small mammal species for the four sampling periods at each study area. Species richness was

measured by the total number of species sampled (Krebs 1989). Species diversity was measured by Simpson's index of diversity (Simpson 1949) which is sensitive to changes in the more abundant species. Simpson's index is the probability of picking two organisms at random that are different species and ranges from 0 to almost 1. The Shannon-Wiener index of diversity (Pielou 1966) was also used since it is sensitive to changes in the rare species in a community sample (Peet 1974). This index is based on information theory and the degree of difficulty in predicting correctly the species of the next individual sampled. This measure increases with the number of species in the community and ranges from 0 to approximately 5.0 for biological communities (Washington 1984). A *t* test (Magurran 1988) allows the diversities (Shannon-Wiener) of the two communities to be compared. Evenness has been measured by scaling each measure of diversity relative to its maximal value when each species in the sample is represented by the same number of individuals (Krebs 1989). All evenness measures range from 0 to 1.

Results

Average population densities per ha of the major species are illustrated in Fig. 1 with *C. rufocanus* and *M. pennsylvanicus* (meadow vole) clearly dominating their respective communities. Average Jolly-Seber population estimates were 100.4 (A) and 104.1 (B) for *C. rufocanus* and 59.3 (A) and 101.6 (B) for *M. pennsylvanicus*. In China, *C. rutilus* (northern red-backed vole) and *Apodemus speciosus* (Japanese field mouse) were at comparable densities (Fig. 1) with Jolly-Seber estimates ranging from 14.7 to 21.2 and 13.1 to 18.0, respectively, for these species. *A. agrarius* (striped field mouse) occurred at densities less than 10/ha. *C. gapperi* (boreal red-backed vole) was the second most abundant species at the Canadian study area (Fig. 1) with Jolly-Seber estimates of 27.0 (A) and 31.2 (B). *P. maniculatus* (deer mouse) occurred at densities of 8.0 to 26.3 (MNA) with Jolly-Seber estimates of 12.0 (A) and 29.0 (B).

Total number of individuals captured for each species over the four sampling periods of each study area is another method used to compare these communities (Table 1). This comparison shows a similar pattern for the major species as discussed for Fig. 1. One shrew species (*Sorex araneus*) appeared at the Langxiang study area with

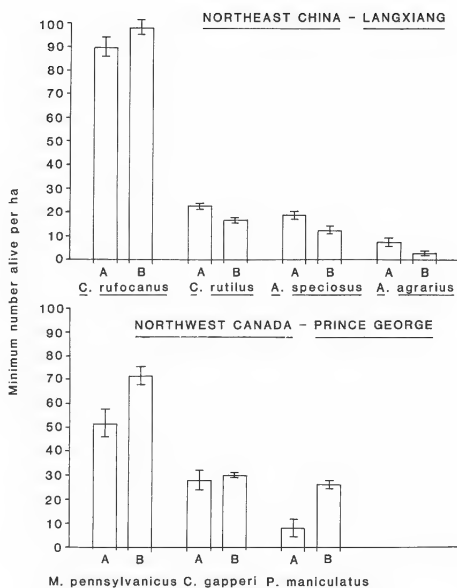


Figure 1. Average population densities (minimum number alive per ha) $\pm$ standard error for the major small mammal species on grids A and B at Langxiang and Prince George study areas.

S. monticolus and *S. cinereus* recorded at Prince George. In addition, a rare species, the northern bog lemming (*Synaptomys borealis*), occurred at the Canadian study area along with weasels of the genus *Mustela*. It is interesting to note that total numbers captured for each community were very similar.

Total biomass for each small mammal species tended to follow the same pattern as recorded for total number of individuals (Table 2). Overall, a greater biomass of prey species were available for predators at Langxiang (5.327 kg) than Prince George (4.208 kg). This larger biomass at Langxiang may be attributed to the significantly larger average body weights of *C. rufocanus* than *M. pennsylvanicus*, and the considerably larger *A. speciosus* than its North American counterpart *P. maniculatus* (Fig. 2).

Species richness was 1.33 times higher for small mammals at Prince George than Langxiang but diversity indices were similar (Shannon-Wiener *t* test = 1.39, *P* = 0.17) (Table 3). In addition, evenness measures were similar.

TABLE 1. Total numbers of individuals captured for each small mammal species based on an average of the two grids at each study area.

Langxiang		Prince George	
Species	Number	Species	Number
<i>Clethrionomys rufocanus</i>	134.0	<i>Microtus pennsylvanicus</i>	111.0
<i>Clethrionomys rutilus</i>	29.5	<i>Clethrionomys gapperi</i>	49.5
<i>Apodemus speciosus</i>	29.0	<i>Peromyscus maniculatus</i>	29.0
<i>Apodemus agrarius</i>	12.0	<i>Microtus longicaudus</i>	1.5
<i>Eutamias sibiricus</i>	1.5	<i>Synaptomys borealis</i>	1.0
<i>Sorex araneus</i>	1.0	<i>Sorex monticolus</i>	11.0
		<i>Sorex cinereus</i>	3.0
		<i>Mustela</i> spp.	3.5
Totals	207.0		209.5

TABLE 2. Total biomass/ha (g) of each small mammal species (single or average weight for each individual) based on an average of the two grids at each study area.

Langxiang		Prince George	
Species		Species	
<i>C. rufocanus</i>	3,568.2	<i>M. pennsylvanicus</i>	2,674.2
<i>C. rutilus</i>	553.3	<i>C. gapperi</i>	878.1
<i>A. speciosus</i>	875.0	<i>P. maniculatus</i>	544.3
<i>A. agrarius</i>	223.4	<i>M. longicaudus</i>	45.5
<i>E. sibiricus</i>	107.0	<i>S. borealis</i>	20.5
<i>S. araneus</i>	—	<i>S. monticolus</i>	37.5
		<i>S. cinereus</i>	8.0
Total	5,326.9		4,208.1

TABLE 3. Species richness, diversity indices, and evenness for small mammals in terms of the total number of individuals captured based on average of the two grids at each study area.

	Langxiang	Prince George
No. of species	6	8
Simpson's index of diversity	0.54	0.64
Evenness	0.65	0.73
Shannon-Wiener index of diversity	1.64	1.87
Evenness	0.63	0.62

Discussion

Study design

Three basic assumptions underlying the study design were (1) the two study areas, although on different continents, had similar temperate climatic conditions and vegetation structure in terms of successional stage after forest harvesting, (2) the sampling grids were true replicates at each area, and (3) the different sampling intervals were not likely an important factor. In terms of the first assumption, the successional stages ranged from 7-10 years of age and there was a remarkable similarity in plant species richness for herbs (Langxiang: 25 species; Prince George: 31 species) and shrubs

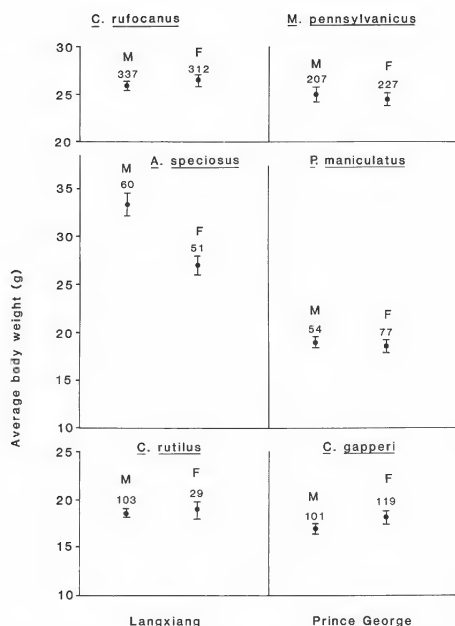


Figure 2. Average body weights and 95% confidence limits of males (M) and females (F) for each of the major small mammal species at Langxiang and Prince George. Sample sizes are above upper confidence limits.

(Langxiang: 16 species; Prince George: 14 species) between the two areas (unpubl. data). This similarity in vegetation was reflected in similar population levels and biomass of small mammals. The replicate sampling grids yielded average values used to make comparisons between areas (Hurlbert 1984). As for the third assumption, although different sampling intervals were used, the actual sampling was conducted over a relatively short period (1-2 months) with the same number of trapping periods at each area. Thus, a relatively representative sample of population data was collected for each community.

Small mammal communities

Small mammal communities in both Langxiang and Prince George had generally high populations of all species in their respective sampling years. The dominant species at Langxiang, *C. rufocanus*, has a 3-year fluctuation in abundance which appears to be synchronous across northeast China (Shu *et al.* 1975). In addition to this brown-backed vole, populations of *C. rutilus*, *A. speciosus*, and *A.*

agrarius were also peaking in 1986, and this pattern occurred again in 1989, but at relatively lower populations of all species compared to 1986 levels (Sullivan *et al.* unpubl.). The dominant species at Prince George was *M. pennsylvanicus*, which like other voles of this genus in North America tends to fluctuate on a 3-4 year cycle (Krebs and Myers 1974). As in northeast China in 1986, all major species at Prince George were at high levels in 1987. Clearly, in both these communities, there must be one or more driving factors which produce favourable conditions and synchronize high populations of all the major species.

C. rufocanus appears to be the counterpart of *M. pennsylvanicus* and indeed, they prefer similar habitats dominated by grasses and herbaceous species with some shrubs on cutover forest lands (Banfield 1974, Shu 1981, 1985, Sullivan and Martin 1991). A species in the genus *Microtus* does live in forests of northeast China, the reed vole (*M. fortis*), but is restricted to wet lowlands and meadows (Allen 1940). *A. speciosus* has similar general habitat requirements as *P. maniculatus*, particularly with respect to a variety of successional forest stages and a catholic diet (Baker 1968; Smirnov 1970). *A. sylvaticus*, the wood mouse, of Europe and Asia is a very similar species to *A. speciosus*, and is very much the "deer mouse" or "white-footed mouse" of the Eurasian continent (Montgomery 1989). *A. agrarius* is primarily associated with agricultural habitats and occurs mainly in forests bordering on cultivated fields (Hsia 1958). The two red-backed voles, *C. rutilus* and *C. gapperi*, are both secondary species within cutover forest habitats with neither species reaching population densities similar to *C. rufocanus* or *M. pennsylvanicus*.

Species richness and diversity

The higher species richness at Prince George than Langxiang was caused by the additional species of shrew and the weasels. However, there was little difference in the measures of diversity. Although not appearing in the samples, three species of *Mustela* occur at the general Langxiang study area: *M. sibirica* (Siberian or yellow weasel), *M. altaica* (black-yellow weasel), and *M. nivalis* (silver-white weasel). In addition, the marten (*Martes flavigula*) and the badger (*Meles meles*) complete the mustelid community of predators (Tate 1947). This community is very similar to Prince George where

again, there are three species of *Mustela*: *M. erminea* (short-tailed weasel), *M. frenata* (long-tailed weasel), and *M. nivalis* (least weasel), along with the pine marten (*Martes americana*) and fisher (*Martes pennanti*) (Banfield 1974).

The most significant finding of this study is the remarkable similarity in relative abundance and diversity of small mammal species occupying young cutover forest lands of mixed coniferous and deciduous species in northeast China and northwest Canada. Because of this similarity, it is not surprising that the mustelid predator communities are also quite comparable. It is likely that similar factors are regulating the population fluctuations of these small mammals in temperate areas of Asia and North America. This is particularly relevant to an understanding of the relationships of these small mammal communities to forest succession

and management. Perhaps the principles of managing temperate forests for wildlife diversity in North America could be applied to similar forests in Asia.

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Literature Cited

- Allen, G. M. 1940. The Mammals of China and Mongolia. In: Natural History of Central Asia. Edited by W. Granger. The American Museum of Natural History, New York. pp. 858-860.
- Banfield, A. W. F. 1974. The Mammals of Canada. University of Toronto Press, Toronto. 438 p.
- Baker, R. H. 1968. Habitats and distribution. In: Biology of *Peromyscus* (Rodentia). Edited by J. A. King. Am. Soc. of Mammal. Spec. Publ. No. 2, pp. 125-167.
- Burger, D. and S. Zhao. 1988. An introductory comparison of forest ecological conditions in Northeast China and Ontario. For. Chron. 64:105-115.
- D'Anieri, P., D. M. Leslie, and L. M. McCormack. 1987. Small mammals in glyphosate-treated clearcuts in northern Maine. Can. Field-Nat. 101:547-550.
- Gashwiler, J. S. 1970. Plant and mammal changes on a clear-cut in west Oregon. Ecology 51:1018-1026.
- Hooven, E. F. 1973. Effects of vegetation changes on small forest mammals. In: Even-age management. Edited by R. K. Hermann and D. P. Lavender. School of Forestry, Oregon State University, Corvallis. pp. 75-97.
- Hooven, E. F. and H. C. Black. 1976. Effects of some clear-cutting practices on small mammal populations in western Oregon. Northwest Sci. 50:189-208.
- Hsia, W. 1958. On the changing tendencies of the rodent population in the recent cut-over land at Dailing, northeast China. Acta Zool. Sin. 10:431-437.
- . 1966. Population dynamics of small rodents Dailing Forest Region, Lesser Khingan mountains. II. The influences of the climatological factors on the numbers of rodents. Acta Zool. Sin. 18:8-18.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187-211.
- Jolly, G. M. and J. M. Dickson. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. Can. J. Zool. 61:922-927.
- Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. 36:239-273.
- . 1989. Ecological Methodology. Harper and Row Publishers, New York. 654 p.
- Krebs, C. J. and J. H. Myers. 1974. Population cycles in small mammals. Adv. Ecol. Res. 8:267-399.
- Magurran, A. E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, New Jersey. 179 p.
- Martell, A. M. 1983. Changes in small mammal communities after logging in north-central Ontario. Can. J. Zool. 61:970-980.
- Martell, A. M. and A. Radvanyi. 1977. Changes in small mammal populations after clearcutting of northern Ontario black spruce forest. Can. Field-Nat. 91:41-46.
- Meidinger, D. and J. Pojar. 1991. Ecosystem of British Columbia. Ministry of Forests. Special Report Series 6. 330 p.
- Montgomery, W. I. 1989. *Peromyscus* and *Apodemus*: Patterns of similarity in ecological equivalents. In: Advances in the Study of *Peromyscus* (Rodentia). Edited by G. L. Kirkland and J. N. Layne. Texas Tech. University Press, Lubbock, Texas. pp. 293-366.
- Peet, R. K. 1974. The measurement of species diversity. Annu. Rev. Ecol. Syst. 5:285-307.
- Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13:131-144.
- Richardson, S. D. 1990. Forests and Forestry in China. Island Press, Covelo, California. 353 p.
- Seber, G. A. 1982. The estimation of animal abundance and related parameters. 2nd ed. Charles Griffin & Co. Ltd., London.
- Shu, F. 1981. Numbers of *Clethrionomys rufocanus* under different forest canopy densities, and their significance in young forest protection. Acta Theriol. Sin. 1:45-50.
- . 1985. On the number of the large-toothed red-back voles (*Clethrionomys rufocanus*) on different slopes and its meaning in rodent pest prevention for young forests. Acta Theriol. Sin. 5:263-267.

- Shu, F., K. Yang, M. Guo, Y. Lui, F. Tian, and C. Li. 1975. The rodent pest in Yichun forest region and our opinions of pest forecasting. *Acta Zool. Sin.* 21:9-17.
- Simpson, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- Smirnov, E. N. 1970. Feeding habits of large Japanese field mouse, large-toothed red-backed vole, and northern red-backed vole in forests of the middle part of the Sikhotealin' Range. *Ekologiya* 6:106-107.
- Sullivan, T. P. 1990. Demographic responses of small mammal populations to a herbicide application in coastal coniferous forest: population density and resiliency. *Can. J. Zool.* 68:874-883.
- Sullivan, T. P. and W. L. Martin. 1991. Influence of site factors on incidence of vole and lemming feeding damage to forest plantations. *West. J. Appl. For.* 6:64-67.
- Tate, G. H. H. 1947. *Mammals of Eastern Asia*. The Macmillan Company, New York. pp. 144-151.
- Washington, H. C. 1984. Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. *Water Res.* 18:653-694.

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Prevalence of *Sarcocystis* in Elk (*Cervus elaphus*) in Oregon

Abstract

The prevalence of *Sarcocystis* spp. in free-ranging elk (*Cervus elaphus*) has been reported in Canada, and in the United States in California, Montana, Washington and Wyoming. Most of these reports involve a relatively small sample size and limited age class of elk. To determine the prevalence of *Sarcocystis* spp. in free-ranging elk in Oregon, heart and/or tongue tissues from 184 elk were examined histologically. The samples were collected from August 1991 to February 1992 from elk ranging in age from 5 days to 12 years. Sarcocysts were present in 178 (97%) of the samples, including 142 of 149 (95%) heart samples, and 115 of 124 (93%) tongues. Tissues from 96% of the males (n=54) and 100% of the females (n=29) contained sarcocysts (101 elk with sex unrecorded). This first report of the prevalence of *Sarcocystis* spp. in elk in Oregon indicates a high infection rate among elk of all ages. Although little is known concerning the pathogenicity of *Sarcocystis* in free-ranging elk and other wild ungulates, the high rate of infection we report in elk, and the widespread and frequent occurrence of this parasite in free-ranging herbivores reported elsewhere in North America, indicate a potential impact on population dynamics and should be considered a potential factor in declining elk populations.

Introduction

Sarcocystis spp. are protozoan parasites which are detected commonly in the muscles of most species of wild and domestic herbivores, and require a predator-prey two-host life cycle. In the intermediate herbivore host (prey), asexual reproduction (schizogony) occurs, and in the definitive carnivore host (predator), sexual reproduction (gametogony) occurs. Coyotes, dogs, foxes, raccoons and wolves are the usual predators, and they become infected by ingesting tissues of an herbivorous intermediate host containing mature sarcocysts. An herbivore becomes infected by ingesting oocysts or sporocysts shed in the feces of an infected predator, resulting in the development of sarcocysts in striated muscles of the heart, tongue, esophagus, diaphragm and skeletal muscles. *Sarcocystis* spp. have been reported in free-ranging elk (*Cervus elaphus*) in North America (Schwartz and Mitchell 1945, Sayama 1952, Pond and Speer 1979, Mahrt and Colwell 1980, Speer and Dubey 1982, Jolley 1982, Dubey *et al.* 1989), with up to 100% infection rate among the animals sampled. Although the percentage of elk infected with *Sarcocystis* spp. was high in these earlier reports, the small sample sizes do not indicate the overall prevalence of *Sarcocystis* spp. in a specific population of elk or in a defined area.

Presently, no information is available on the prevalence of natural infections of *Sarcocystis* spp. in elk in Oregon. To determine the prevalence of *Sarcocystis* spp. in the state, we histologically

examined heart and/or tongue tissues of elk harvested by hunters.

Materials and Methods

Between August 1991 and February 1992, heart and/or tongue tissue samples from 183 elk harvested by hunters and 1 elk found dead from four counties in Oregon (Union, n=161, 45° 30' N, 118° W; Harney, n=11, 43° N, 118° 30' W; Lake, n=10, 43° N, 120° 30' W; Klamath, n=2, 43° N, 121° 30' W) were submitted to the College of Veterinary Medicine Parasitology Laboratory at Washington State University (Figure 1). The elk ranged in age from 5 days to 12 years, with the majority between 1 and 3 years of age. There were 29 females, 54 males, and 101 with sex unrecorded. Tissues were fixed in 10% buffered formalin upon arrival to the laboratory. Approximately 1.5 cm² section of each tissue was embedded in paraffin, sectioned, stained with hematoxylin and eosin, and examined microscopically at 40x for the presence of sarcocysts.

Results and Discussion

Sarcocysts were detected in the tissues (Figure 2) of 178 of the 184 (97%) elk. Tissues of 96% of the males (n=54) and 100% of the females (n=29) contained sarcocysts. Sarcocysts were not detected in the tissues of six elk: a 5-day-old male found dead (heart only), a 6-month-old calf (heart only), a 1.5-year male (heart and tongue), and 3 elk of unknown age and sex (tongues only). The 1.5-year male was from Harney County, and the other five from Union county. Sarcocysts were detected in 142 of 149 (95%) hearts and 115 of 124

¹To whom reprint requests should be addressed.

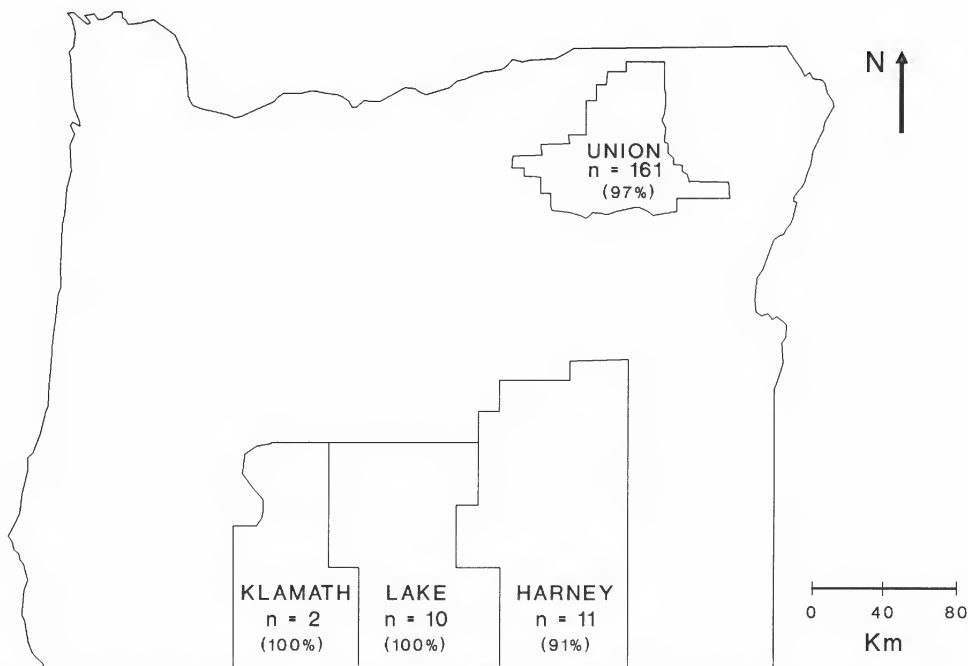


Figure 1. Counties within Oregon from which elk tissues were obtained. Percentage of elk infected with *Sarcocystis* spp. in parenthesis.

(93%) tongues. Of the 89 elk for which tissues of both heart and tongue were submitted, 79 (88.8%) were positive in both tissues and only 1 (1.1%) was found to be negative for sarcocysts in both. Among the 9 elk in which sarcocysts were found in only one of the tissues, 4 (4.5%) were negative in heart and 5 (5.6%) were negative in tongue.

The intensity of sarcocysts present did not appear to be appreciably different between heart and tongue tissues, varying from 1 to approximately 75 per cm². Mean size of 75 heart sarcocysts was 135.7 x 69.6 μ m (range, 34 to 821 x 14 to 240 μ m), and mean size of 75 tongue sarcocysts was 132.8 x 59.6 μ m (range, 24 to 874 x 17 to 152 μ m).

The high prevalence of *Sarcocystis* infection we found in this study of elk in Oregon is in accordance with previous reports of *Sarcocystis* in free-ranging herbivores in other areas of North America (Sayama 1952, Pond and Speer 1979, Mahrt and Colwell 1980, Dubey *et al.* 1989). Keem (1974) found over 90% of the elk in Wyoming to be infected by 1 year of age. During the period of this study, our laboratory also received heart and

tongue tissues from elk harvested by hunters in Meagher County in central Montana (n=4), and Asotin County in southeastern Washington (n=7), and all 11 samples contained *Sarcocystis*.

There are three named species of *Sarcocystis* in elk, and two, *Sarcocystis wapiti* and *S. sybillensis*, have been reported from North America (Dubey *et al.* 1989). *Sarcocystis wapiti* (Speer and Dubey 1982) has a thin (<1 μ m) sarcocyst wall with villar protrusions and has been classified as a Type 2 cyst wall (Dubey *et al.* 1989). The coyote (*Canis latrans*) (Dubey 1980) and the dog (*Canis familiaris*) (Margolin and Jolley 1979) are known definitive hosts. *Sarcocystis sybillensis* (Dubey *et al.* 1983) has a thick (up to 8 μ m) and hairy sarcocyst wall with villar protrusions and has been classified as a Type 8 cyst wall (Dubey *et al.* 1989). The dog is a definitive host (Dubey *et al.* 1983). Based on electron microscopy, at least two species of *Sarcocystis*, including *S. wapiti*, were present in these elk from Oregon. Definitive identification of the second species was not determined.

The significance of *Sarcocystis* infections in free-ranging herbivores has not been determined.

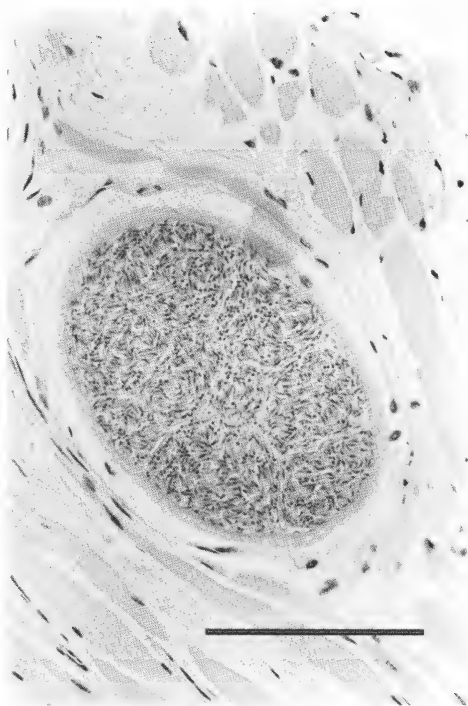


Figure 2. Photomicrograph of *Sarcocystis* sp. in elk heart tissue. Bar = 100 μ m.

Literature Cited

- Dubey, J. P. 1980. Coyote as a final host for *Sarcocystis* species of goats, sheep, cattle, elk, bison and moose in Montana. *Am. J. Vet. Res.* 41:1227-1229.
- Dubey, J. P., W. R. Jolley, and E. T. Thorne. 1983. *Sarcocystis sybillensis* sp. nov. from the North American elk (*Cervus elaphus*). *Can. J. Zool.* 61:737-742.
- Dubey, J. P., C. A. Speer, and R. Fayer. 1989. *Sarcocystosis of animals and man*. CRC Press, Boca Raton, Florida. 215 p.
- Hudkins, G., and T. P. Kistner. 1977. *Sarcocystis hemionilatrantis* (Sp. N.) life cycle in mule deer and coyotes. *J. Wildl. Dis.* 13:80-84.
- Jolley, W. R. 1982. Genus: *Sarcocystis*. In E. T. Thorne, N. Kingston, W. R. Jolley and R. C. Bergstrom (ed.). *Diseases of Wildlife in Wyoming*. Wyoming Game and Fish Department, Cheyenne, WY. Pp. 124-127.
- Keem, M. D. 1974. Some aspects of sarcosporidiosis in Wyoming elk (*Cervus canadensis*). M.S. Thesis, Univ. of Wyoming, Laramie. 81 p.
- Mahrt, J. L., and D. D. Colwell. 1980. *Sarcocystis* in wild ungulates in Alberta. *J. Wildl. Dis.* 16:571-576.
- Margolin, J. H., and W. R. Jolley. 1979. Experimental infection of dogs with *Sarcocystis* from wapiti. *J. Wildl. Dis.* 15:259-262.
- Pond, D. B., and C. A. Speer. 1979. *Sarcocystis* in free-ranging herbivores on the National Bison Range. *J. Wildl. Dis.* 15:51-53.
- Sayama, K. 1952. *Sarcocystis* in deer and elk in California. *California Fish and Game* 38:99-104.
- Schwartz, J. E., and G. E. Mitchell. 1945. The Roosevelt elk on the Olympic Peninsula, Washington. *J. Wildl. Manage.* 9:295-319.
- Speer, C. A., and J. P. Dubey. 1982. *Sarcocystis wapiti* sp. nov. from the North American wapiti (*Cervus elaphus*). *Can. J. Zool.* 60:881-888.

Hudkins and Kistner (1977) proposed that high fawn mortality and declining mule deer (*Odocoileus hemionus*) populations in Oregon might be attributed to *Sarcocystis*. They experimentally inoculated 11 mule deer fawns with large numbers of sporocysts of *Sarcocystis hemionilatrantis*, and 9 fawns died between post-inoculation days 27 and 63. Pond and Speer (1979) suggested that a decline in the number of deer fawns on the National Bison Range in Montana may be partially due to *Sarcocystis* infections. The 97% *Sarcocystis* infection rate we found in elk in Oregon, along with reports of high prevalence in free-ranging herbivores elsewhere, suggests investigations should be conducted to determine the pathogenicity of this parasite in free-ranging herbivores, and its impact upon their populations.

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Trace Element Geochemistry of Volcanic Glass from the Obsidian Cliffs Flow, Three Sisters Wilderness, Oregon

Abstract

This study was undertaken to investigate potential intrasource trace element variability in the Obsidian Cliffs flow, Three Sisters Wilderness, Oregon. Geologic samples of artifact-quality volcanic glass (obsidians) were collected from twelve locations around the flow, and 80 of these (ten each from eight locations) were subjected to non-destructive energy dispersive x-ray fluorescence analysis. Concentration abundances of eleven minor, trace, and rare earth elements were determined for each collection location. The results show that all locations represent obsidian of the same (Obsidian Cliffs) geochemical type, and they contribute to the long-term goal of establishing a geochemical data base against which artifacts from Oregon archaeological sites can be compared.

Introduction

Until quite recently, obsidian studies have attracted little interest from Oregon archaeologists. Consequently, studies in the state have lagged behind those conducted in California where, for the last two decades, archaeologists have reaped the benefits from the partnership forged with geochemists. There archaeologists have employed volcanic glass studies to investigate (among other topics) differences in prehistoric social ranking, prehistoric trade and exchange, and the production histories of obsidian quarries. Despite this lag, the archaeological potential for Oregon obsidian studies is truly exciting, since the state probably contains as many artifact-quality sources of volcanic glass as are known from any region of similar size in the world.

However, before the benefits of obsidian studies (in this case, geochemical "fingerprinting" or "sourcing") can be accrued archaeologically, it is first necessary to locate and geochemically characterize parent geologic sources (and source types), since it is to the geochemical "profiles," or "fingerprints," of these volcanic glasses that measurements on archaeological artifacts will be compared. Despite the initial skepticism for obsidian studies that followed disclosure of mistakes in both x-ray analytical techniques and statistical classifications of obsidian sources and artifacts throughout Oregon (Sappington 1981a,b; Toepel and Sappington 1982; see Hughes 1984), subsequent studies (e.g. Hughes 1986a, b; Skinner 1983) have realized some of the potential of such work, and have charted some promising research directions. But before any confidence can be placed in *archaeological* applications of obsidian studies a solid

geochemical foundation must be established, grounded in analyses reported in internationally recognized measurement units calibrated to international rock standards. It is only through adherence to analytically rigorous standards that researchers can begin to build a quantitative data base for Oregon obsidians that can be shared by researchers at different laboratories.

Recognizing this, the ultimate goal of what has come to be called "obsidian sourcing" research should serve two complementary purposes- the first principally *geochemical*, the second principally *archaeological*. First it is necessary to collect and analyze volcanic glasses and to determine whether any geochemical evidence exists for intrasource variability among quarries. Having accomplished the first step, these base-line geochemical data can be employed to investigate archaeological questions regarding the long-term use-life history of obsidian quarries, prehistoric trade and exchange, and mobility patterns. The research reported here was undertaken to investigate only the first of these two issues.

The Problems

The present study is not the first (see Williams [1944] for a geologic description of the flow) to generate trace element data for Obsidian Cliffs volcanic glass but, compared to the geochemical and archaeometric attention devoted to the nearby Newberry Volcano (e.g. Laidley and McKay 1971; Higgins 1973; Friedman 1977; MacLeod and Sherrod 1988), research on the Cliffs is considerably less extensive and detailed. Despite the work conducted to date, three problems remained which required further research. First, geochemical

measurements on obsidian from the Cliffs (Anttonen 1972; S. Hughes 1983; Skinner 1983) remain unpublished and the results have not been widely disseminated. Second, Obsidian Cliffs glass was characterized on the basis of an extremely small number of analyses; Skinner (1983), for example, reported analyses for only five elements on four samples, but it was not altogether clear to what extent these measurements reflected the range of geochemical variability in the source. Third, analyses undertaken to date were essentially *destructive*; that is, some portion of the geologic specimen was crushed and ground into a fine powder prior to wavelength dispersive x-ray fluorescence (WDXRF; see Skinner 1983: Appendix V, p. 6) and neutron activation analysis. While this procedure has a long history in geochemistry, recent advances in computer-based spectrum deconvolution subroutines and automatic matrix-effect correction programs have enabled those employing energy dispersive x-ray fluorescence (EDXRF) on volcanic glasses to conduct *non-destructive* quantitative analyses of both geologic source samples and archaeological artifacts (see Hughes 1986a, b; 1988a, b). Although traditional WDXRF analysis is capable of detecting slightly lower concentrations of certain elements than state-of-the-art energy dispersive instrumentation, this advantage is offset in *archaeological* applications because portions of artifacts are sacrificed (i.e., ground into a powder) prior to WDXRF analysis (Skinner 1983: Appendix IX, p. 12, 17; see also Nelson [1984: 28]). In light of the close comparison between WDXRF, EDXRF and neutron activation measurements on obsidian from the same sources (see Hughes 1984: Table 3; 1986b: Table 4; 1988a: Table II; Hughes and Nelson 1987: Table 1) and archaeology's explicit conservation ethic, it seemed most appropriate to extend the non-destructive method of analysis to Oregon obsidians—specifically, to the Obsidian Cliffs (see also Hughes 1986a).

Field Reconnaissance and Collection

Obsidian source specimens were obtained from 12 outcrops at, and adjacent to, Obsidian Cliffs (see Figures 1 and 2). Observations were made during the field reconnaissance phase regarding the quality of obsidian at each occurrence, variations in glass texture and color and, in particular, evidence for prehistoric utilization at each location. Although some evidence for prehistoric quarrying was ob-

served at all 12 localities, the intensity of such activities (based on qualitative impressions of the amount of quarry-workshop debris on the surface) varied considerably across collection sites. The field collection phase was designed to obtain samples spanning the full range of visual varieties (i.e., colors and texture variations) in the hope that, if macroscopic variation was encoded geochemically, it might be possible to identify subtle intrasource distinctions. Red-and-black mottled obsidian was collected from an *in-situ* occurrence at a prominence along the western margin of the Obsidian Cliffs flow (location 7106, see Figure 1), while mahogany colored varieties were observed and collected at locations 774, 779 and 789 and 7148. Despite a previously reported occurrence of red obsidian at Obsidian Cliffs (C. Skinner, pers. comm.), the prevailing convention among local archaeologists has been that glass of red or red-and-black physical appearance must have been conveyed from sources to the east of the Cascades (e.g. Glass Buttes) where red obsidians are well-known (C. Davis, pers. comm.).

The choice of particular site collections for subsequent geochemical analysis was influenced by the preceding factors and by the areal extent and abundance of observed quarry-workshop debris. Lacking any clear understanding of the production history of the Obsidian Cliffs quarries (i.e., how long they were used, what kinds of prehistoric manufacturing activities were undertaken at each, whether or not their use-life histories had changed through time), it seemed advisable to focus initial research efforts on the quarries (sites) which had the greatest surface densities of artifact manufacturing debris on the assumption that such densities could serve as general indicators of the importance of each source in the past. Consequently, of the twelve collecting locations, samples from eight (nos. 774, 775, 777, 778, 782, 7106, 7138, and 7148 on Figure 2) were later subjected to x-ray fluorescence analysis.

Laboratory Analysis: Methods

Laboratory investigations were performed on a Spectrace™ 5000 (Tracor X-ray) energy dispersive x-ray fluorescence spectrometer equipped with a rhodium (Rh) x-ray tube, a 50 kV x-ray generator, and a Si(Li) solid state detector with 150 eV resolution (FWHM) at 5.9 keV in a 30 mm² area. The x-ray tube was operated at 30.0 kV, 0.30 mA,



Figure 1. Aerial view to southeast across the Obsidian Cliffs flow (lower left in photo), with Collier Cone and the North Sister in background. Arrow specifies the terminus of the flow, which corresponds with collection location 7106 on Figure 2.

using a 0.127 mm Rh primary beam filter in an air path at 200 seconds livetime to generate x-ray intensity data for elements Zn ($K\alpha$), Ga ($K\alpha$), Rb ($K\alpha$), Sr ($K\alpha$), Y ($K\alpha$), Zr ($K\alpha$), and Nb ($K\alpha$). Ti ($K\alpha$), Mn ($K\alpha$), and total iron ($Fe_2O_3^T$) intensities were generated by operating the x-ray tube at 15.0 kV, 0.30 mA, with a 0.127 mm aluminum (Al) filter in an air path at 200 seconds livetime, while Ba ($K\alpha$) intensities were generated by operating the x-ray tube at 50.0 kV, 0.35 mA, with a 0.63 mm copper (Cu) filter at 300 seconds livetime. Trace

element intensities were converted to concentration estimates by employing a least-squares calibration line established for each element from analysis of up to 25 international rock standards certified by the U.S. Geological Survey, the U.S. National Institute of Standards and Technology, the Geological Survey of Japan, and the Centre de Recherches Petrographiques et Geochimiques (France). Further details pertaining to x-ray tube operating conditions, calibration and element-specific detection limits appear in Hughes (1988a). The x-ray analyses were

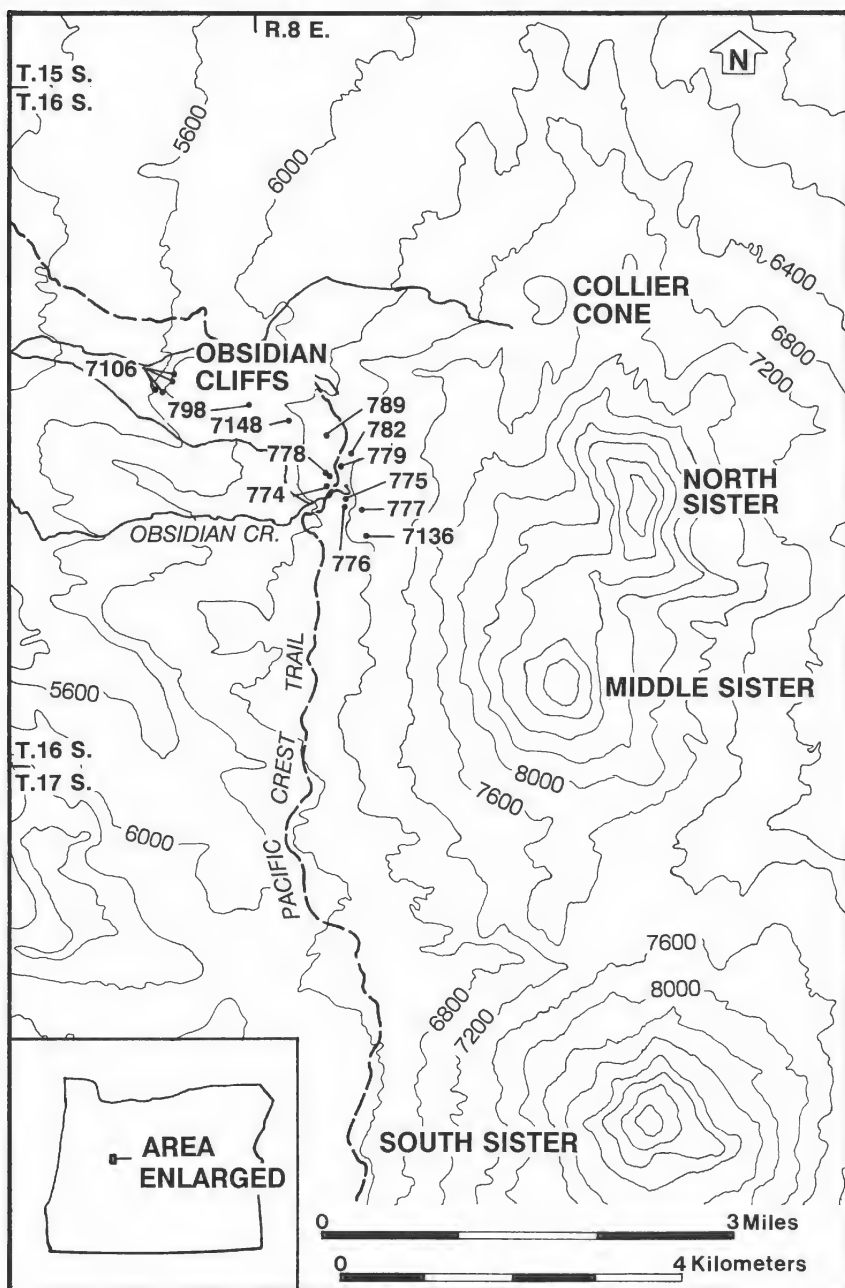


Figure 2. The state of Oregon (inset) showing the location of the study area in the Cascade Range. Numbers around Obsidian Cliffs refer to the sites from which geologic samples were collected (see Table 1).

TABLE 1. Trace, rare earth and selected minor element contents of volcanic glass collected from eight areas at Obsidian Cliffs (see Figure 2 for locations). All elemental values in parts per million, except iron (Fe), expressed as total iron (Fe_2O_3^T) in weight percent. $\bar{X}$ = sample mean; S.D. = sample standard deviation; CV% = coefficient of variation. Ten specimens analyzed from each site. Site numbers assigned by Willamette National Forest personnel.

Element		Collection Locations							
		774	775	777	778	782	7106	7136	7148
Ti	$\bar{X}$	597	604	596	616	586	627	615	612
	S.D.	37	31	22	52	37	24	36	53
	CV%	6	5	4	8	6	4	6	9
Mn	$\bar{X}$	384	383	381	378	382	378	384	390
	S.D.	12	9	8	5	10	7	9	7
	CV%	3	2	2	1	3	2	2	2
Fe_2O_3^T	$\bar{X}$	1.20	1.22	1.22	1.20	1.21	1.19	1.21	1.24
	S.D.	.03	.03	.03	.02	.03	.01	.03	.06
	CV%	2	2	2	1	3	1	2	4
Zn	$\bar{X}$	45	43	45	43	41	42	45	46
	S.D.	6	5	5	3	6	4	7	5
	CV%	13	11	11	6	13	10	14	11
Ga	$\bar{X}$	16	16	17	18	18	18	17	16
	S.D.	2	3	2	1	2	1	3	3
	CV%	11	17	11	6	12	8	18	16
Rb	$\bar{X}$	76	76	78	76	75	78	77	75
	S.D.	2	3	3	2	3	2	3	2
	CV%	3	3	4	2	3	2	3	3
Sr	$\bar{X}$	101	102	102	103	102	102	102	106
	S.D.	4	3	2	4	5	3	4	6
	CV%	4	3	2	4	5	3	4	6
Y	$\bar{X}$	18	18	18	18	18	17	17	18
	S.D.	1	1	1	1	1	1	1	1
	CV%	4	4	7	6	6	7	6	8
Zr	$\bar{X}$	88	85	88	87	86	88	89	92
	S.D.	2	2	3	3	5	5	3	5
	CV%	3	2	3	3	5	6	3	5
Nb	$\bar{X}$	7	8	8	8	8	9	9	8
	S.D.	2	2	2	2	3	2	3	3
	CV%	26	23	28	23	33	23	30	32
Ba	$\bar{X}$	877	845	899	821	866	824	851	897
	S.D.	33	23	34	20	21	36	45	29
	CV%	4	3	4	3	3	4	5	3

completely non-destructive; cortex-free obsidian flakes and chunks were detached from geologic samples and each was rinsed in distilled water to remove any possible surface contaminants.

Laboratory Analysis: Results

Trace element values generated for 80 samples from eight sampling locations appear in Table 1.

Examination of sample means and standard deviations reveals that all eight sites contain obsidian of remarkably uniform geochemical composition; in fact, mean values for all eight of the best measured elements overlap at two sigma. Thus, there is sound justification for concluding that these eight locations represent exposures of obsidian of the same geochemical type. The values in Table 1 also

are in very close agreement with those generated on a small number of Obsidian Cliffs samples by Skinner (1983: Appendix X), illustrating that non-destructive quantitative EDXRF provides concentration estimates congruent with those generated using the destructive WDXRF technique.

The present study greatly expands the number of minor, trace and rare earth element measurements for Obsidian Cliffs glass (from five in Skinner's study to eleven in Table 1 herein), and these additional elements will likely be of assistance in helping to distinguish between Obsidian Cliffs glass and other obsidians which have similar Rb, Sr, and Zr compositions (e.g. Inman Creek Gravels, Group B; Skinner 1983). The trace element data in Table 1 are quite different from artifact-quality obsidians from the nearby Newberry Volcano (see Table 2; cf. MacLeod and Sherrod [1988: Table 1]) and with the porphyritic microvesicular obsidians of the South Sister in the Cascade Range (Macdonald et al 1992: Appendix 1, [specimens 8-10], p.170). The geochemical contrasts among sources are illustrated in Figure 3 using a bivariate plot of Zr vs. Sr abundance.

Discussion

Although quantitative measurements (values reported in parts per million [ppm] and weight percent [%] composition) are reported here for eleven minor, trace and rare earth elements, not all elements are equally useful in obsidian characterization studies. The best elements to employ for inter-source discrimination are those I term "diagnostic" (see also Hughes 1990)- those minor, trace, and/or rare earth elements that are well-measured by x-ray fluorescence, and whose concentrations show low variability *within* a source and marked variability *across* sources. Diagnostic elements are those whose concentration values allow one to draw the clearest geochemical distinctions between sources. In practice, the actual identification of a diagnostic element and suites of diagnostic elements is influenced not only by instrument sensitivity and analytical technique (e.g., x-ray fluorescence vs. neutron activation), but by the concentration of a particular element in a source under study.

TABLE 2. Trace element geochemistry of seven obsidians in the vicinity of the Newberry Volcano, Oregon. All values in parts per million (ppm), except iron (Fe) expressed as Fe_2O_3^T in weight percent; $\bar{X}$ = sample mean, S.D. = sample standard deviation, CV% = coefficient of variation (in percent). Five specimens were analyzed from each source, except McKay Butte (n=3).

Element		Big Obsidian Flow (188-)	Game Hut (189-)	Pumice Cone (191-)	North Flow (190-)	East Lake (192-)	McKay Butte	Quartz Mtn.
Ti	$\bar{X}$	1350	1385	1416	1358	1475	1165	568
	S.D.	52	55	66	65	70	48	31
	CV%	4	4	5	5	5	4	6
Mn	$\bar{X}$	589	455	466	447	466	387	376
	S.D.	12	18	11	24	12	3	4
	CV%	2	4	2	5	3	1	1
Fe_2O_3^T	$\bar{X}$	2.60	2.25	2.29	2.23	2.36	1.97	1.84
	S.D.	.05	.06	.05	.09	.05	.04	.03
	CV%	2	3	2	4	2	2	2
Rb	$\bar{X}$	117	127	126	129	126	125	130
	S.D.	1	6	3	7	4	5	5
	CV%	1	5	3	6	4	4	4
Sr	$\bar{X}$	53	60	59	59	62	59	61
	S.D.	2	3	4	3	3	2	2
	CV%	4	5	6	5	4	3	3
Y	$\bar{X}$	42	38	39	37	36	35	38
	S.D.	1	3	3	3	2	1	2
	CV%	3	8	6	7	6	4	5
Zr	$\bar{X}$	349	277	275	274	275	195	178
	S.D.	3	7	7	6	8	8	4
	CV%	1	3	2	2	3	4	2

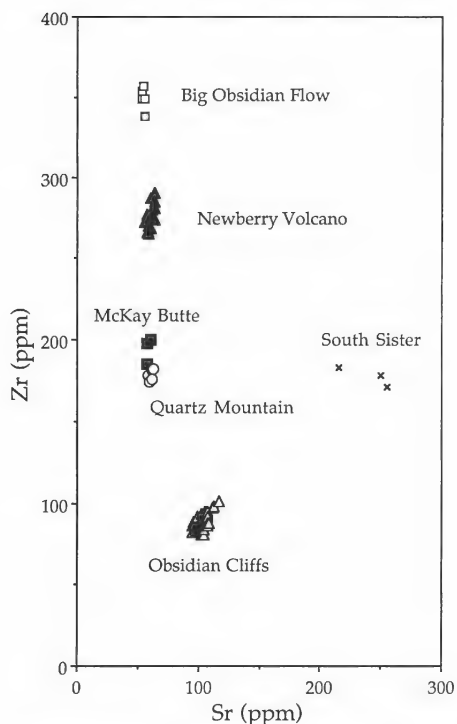


Figure 3. Bivariate plot of Zr vs. Sr abundances in five major Cascade Range obsidian source (chemical) types. Plots made from raw data summarized in Tables 2 and 3 herein, except South Sister (data from Macdonald et al. 1992: Appendix 1, p. 128, specimens 8-10). Open squares represent obsidian from the Big Obsidian Flow, Newberry Volcano; filled triangles represent four source localities (Game Hut, Pumice Cone, North, and East Lake flows) in the Newberry Volcano; filled squares represent McKay Butte; open circles Quartz Mountain; and open triangles depict Obsidian Cliffs obsidian. South Sister porphyritic microvesicular obsidian is represented on the diagram by x symbols.

For example, Sr is in most cases an extremely useful trace element in obsidian sourcing studies because it can be measured with good precision using x-ray fluorescence analysis and its concentrations vary by several orders of magnitude across sources (Jack and Carmichael 1969: 22; Macdonald et al. 1992: 103). Occasionally, however, Sr content may not be diagnostic for glasses containing $\leq$ ca. 10-15 ppm because such concentrations are near the calibration-imposed detection limits of x-ray fluorescence instrumentation (e.g., Dog Hill obsidian [Hughes 1986a: Table 2]). In

the Obsidian Cliffs case, Sr is a diagnostic element since it occurs in concentrations considerably above detection limits, it varies markedly across sources, and coefficients of variation (see Hughes 1984) for all Obsidian Cliffs collection sites show that it is measured with precision. On the basis of measurement precision (as monitored by CV% values; Table 1), Ti, Mn, Fe_2O_3^T , Rb, Y, Zr and Ba also could be considered diagnostic elements. Zn, Ga and Nb ppm concentrations also were measured and reported for each collection location, but these elements are not considered diagnostic because they do not usually vary significantly across obsidian sources (see Hughes 1982, 1984, 1986b), and because coefficients of variation for these three elements are much larger than those of the remaining eight. Although Zn, Ga and Nb were not diagnostic elements in this particular study, each element has to be evaluated on a case-by-case basis since it is clear that volcanic glasses occur in which some of these (e.g., Nb in certain Idaho [Nelson 1984: Table 5, source #38], Arizona [Jack 1971: Table 1] and New Mexico [Hughes 1988b] obsidians) and other elements (e.g., Sn in certain Peruvian obsidian [Macdonald et al. 1992: Appendix 1, specimen 160]) can serve in a diagnostic capacity.

Conclusions

There are several points that should be made with regard to these geochemical findings. To the extent that this uniform minor, trace and rare earth element profile monitors underlying geochemical homogeneity, it should now be possible to pursue obsidian hydration studies to address questions relating to the use-life history of the Obsidian Cliffs source since the probability of intrasource heterogeneity of sufficient magnitude to affect obsidian hydration rate development now appears exceedingly slight. Major and minor element composition data to support this conclusion appear in Skinner (1983: Appendix VII, Table VII-1). Likewise, the geochemical uniformity across all toolstone-caliber varieties of Obsidian Cliffs volcanic glass suggests, as has been documented elsewhere in North America (Griffin et al. 1969; Jackson 1974; Hughes 1986b), that color of obsidian (i.e. red vs. black) carries little significance in provenance studies. The present study underscores again that there is no geochemical justification for the presumption that, in Willamette Valley sites, for example, red obsidian must have been procured

from sources to the east of the Cascades since it couldn't be obtained "locally" (i.e., at Obsidian Cliffs or in its derived river gravels).

Finally, beyond their immediate geochemical utility of contributing to the establishment of a comprehensive multi-element regional data base for Oregon obsidians to which archaeological artifacts can be compared, these geochemical data promise to be pivotal in subsequent archaeological studies; in particular those concerned with reconstructing synchronic and diachronic aspects of prehistoric procurement and conveyance systems (trade and exchange), studies focusing on change and stability in prehistoric settlement subsistence systems and population mobility, and research directed toward identifying functional and temporal variability in the obsidian tool production history of the Obsidian Cliffs.

Literature Cited

- Anttonen, G. J. 1972. Trace elements in the High Cascade volcanic rocks, Three Sisters area, Oregon. Stanford University. Ph.D. Dissertation.
- Friedman, I. 1977. Hydration dating of volcanism at Newberry Crater, Oregon. U.S. Geol. Surv. J. Res. 5: 337-342.
- Griffin, J. B., A. A. Gordus, and G. A. Wright. 1969. Identification of the sources of Hopewellian obsidian in the Middle West. *Amer. Antiquity* 34: 1-14.
- Higgins, M. W. 1973. Petrology of Newberry Volcano, Oregon. *Bull. Geol. Soc. Amer.* 84: 455-488.
- Hughes, R. E. 1982. Age and exploitation of obsidian from the Medicine Lake Highland, California. *J. Archaeol. Sci.* 9: 173-185.
- . 1984. Obsidian sourcing studies in the Great Basin: problems and prospects. In Richard E. Hughes (ed.) *Obsidian Studies in the Great Basin*. Contrib. Univ. Calif. Archaeol. Res. Facil. 45: 1-19.
- . 1986a. Energy dispersive x-ray fluorescence analysis of obsidian from Dog Hill and Burns Butte, Oregon. *Northw. Sci.* 60: 73-80.
- . 1986b. Diachronic variability in obsidian procurement patterns in northeastern California and southcentral Oregon. *Univ. Calif. Publ. Anthropol.* 17.
- . 1988a. The Coso volcanic field reexamined: implications for obsidian sourcing and hydration dating research. *Geoarchaeol.* 3: 253-265.
- . 1988b. Archaeological significance of geochemical contrasts among southwestern New Mexico obsidians. *Texas J. Sci.* 40: 297-307.
- . 1990. Obsidian sources at James Creek Shelter, and trace element geochemistry of some northeastern Nevada volcanic glasses. In R. G. Elston and E. Budy (eds.), *The Archaeology of James Creek Shelter*. Univ. Utah Anthropol. Pap. 115: 297-305.
- Hughes, R. E., and F. W. Nelson. 1987. New findings on obsidian source utilization in Iowa. *Plains Anthropol.* 32: 313-316.
- Hughes, S. S. 1983. Petrochemical evolution of High Cascade volcanic rocks in the Three Sisters Region, Oregon. Oregon State University, Corvallis. Ph.D. Dissertation.
- Jack, R. N. 1971. The source of obsidian artifacts in northern Arizona. *Plateau* 43: 103-114.
- . 1976. Prehistoric obsidian in California I: geochemical aspects. In R. E. Taylor (ed.), *Advances in Obsidian Glass Studies: Archaeological and Geochemical Perspectives*, Noyes Press, Park Ridge, New Jersey. Pp. 183-217.
- Jack, R. N., and I. S. E. Carmichael. 1969. The chemical 'fingerprinting' of acid volcanic rocks. *Calif. Div. Mines and Geol. Spec. Rept.* 100: 17-32.
- Jackson, T. L. 1974. The economic of obsidian in central California prehistory: applications of x-ray fluorescence spectrography in archaeology. Department of Anthropology, San Francisco State University. M.A. Thesis.
- Laidley, R. A., and D. S. McKay. 1971. Geochemical examination of obsidians from the Newberry Caldera, Oregon. *Contrib. Mineral. Petrol.* 30: 336-342.
- Macdonald, R., R. L. Smith, and J. E. Thomas. 1992. Chemistry of the subalkalic silicic obsidians. U. S. Geol. Surv. Prof. Paper 1523.
- MacLeod, N. S., and D. R. Sherrod. 1988. Geologic evidence for a magma chamber beneath Newberry Volcano, Oregon. *J. Geophys. Res.* 93: 10,067-10,079.
- Nelson, F. W., Jr. 1984. X-ray fluorescence analysis of some western North American obsidians. In Richard E. Hughes (ed.), *Obsidian Studies in the Great Basin*. Contrib. Univ. Calif. Archaeol. Res. Facil. 45: 27-62.
- Sappington, R. L. 1981a. A progress report on the obsidian and vitrophyre sourcing project. *Idaho Archaeol.* 4: 4-17.
- . 1981b. The archaeology of the Lytle Gulch site (10-AA-72): prehistoric occupation in the Boise River Canyon, southwestern Idaho. Univ. Idaho Res. Manuscript Ser. 66.

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Skinner, C. 1983. Obsidian studies in Oregon: an introduction to obsidian and an investigation of selected methods of obsidian characterization utilizing obsidian collected at prehistoric quarry sites in Oregon. University of Oregon, Eugene. M.A. Thesis.

Toepel, K.A., and R. L. Sappington. 1982. Obsidian use in the Willamette Valley: trace element analysis of obsidian from the Halverson site. *Tebiwa* 19: 27-40.

Williams, H. 1944. Volcanoes of the Three Sisters region, Oregon Cascades. *Univ. Calif. Publ. Geol. Sci.* 27: 37-84.

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EDITOR'S NOTE: The following article by Dr. Stewart Ware was originally published in the *ASB Bulletin* (*ASB Bulletin* 37:22-28, 1990). Dr. Gerry Wright recently showed me this article, and I felt that the discussion on the value of regional journals was particularly relevant for the readership of *Northwest Science*. The article is reprinted here with permission of the author and Dr. Frank Schwartz, Editor of the *ASB Bulletin*.

Stewart Ware, Department of Biology, College of William and Mary, Williamsburg, Virginia 23185

Prestige and Impact vs. Usefulness in Biological Journals or Am I Just a Regional Kind of Guy?

Abstract

The impact factor and citation half-life for scientific journals, as calculated by Science Citation Index, is used by some college administrators and department chairs to indicate the prestige of a journal, and thus the "significance" of articles published in these journals by faculty members. Regional journals, published by associations or societies interested in the botany or natural history of specific geographical areas, are likely to have lower impact factors and thus lower prestige than journals with national or international geographical coverage. Evidence is presented that from the standpoint that the journals (a) regularly have articles pertinent to one's research, (b) are likely to be cited in one's articles, (c) are likely to cite one's articles, and (d) are seen by a readership interested in one's research, regional journals may be as useful or even more useful to field biologists than some far more prestigious journals. Administrators and department chairs who are not aware of this need to be enlightened.

The merit review policy at the College of William and Mary has long required that faculty members show "evidence of continuing contribution to scholarship" through publication in peer-reviewed journals. Most of the Department of Biology faculty have been quite happily complying with that requirement, publishing from time to time in various journals, both alone and jointly with graduate or undergraduate students. Several years ago, all faculty members received a request from the Dean that they provide him with a ranking "in order of prestige" of the journals in their research area. The implication was clear. "Evidence of continuing contribution to scholarship" would no longer be meritorious in itself; one would now have to make this contribution through "prestigious" journals.

Difficulties arose immediately in trying to provide a ranking of journals in my field, for there is often a difference between the defined content of a journal and the usual content of its issues. The *American Journal of Botany* and *Botanical Gazette* are both prestigious general botanical journals covering many botanical subject areas. There are, however, relatively few articles in either dealing with forest vegetation (my primary area of interest). This is not because either refuses to accept vegetation papers, for excellent vegetation papers do appear (at long intervals) in both of them. However, custom and readership interests have directed

their usual contents away from the vegetation area. Therefore, both in terms of finding articles directly pertinent to one's vegetation research and in terms of being assured of a readership particularly interested in vegetation ecology, these two journals would be less *useful* to a vegetation scientist than the general botanical journals *Bulletin of the Torrey Botanical Club*, *Castanea*, (in the east) and *Madroño* (in the west), or the natural history journal *American Midland Naturalist*. These four journals are quite likely to have articles on vegetation in each issue, and on the assumption that this means an interested readership will see the article, vegetation ecologists may be more likely to submit their manuscripts to one of these four journals than to the first two.

Should the Dean be told that the *American Journal of Botany* is perhaps the most prestigious general botanical journal, but that I never submit vegetation articles there, thus perhaps giving him the impression that I don't think my work is of prestige quality? Should he be told that this is the most prestigious general botanical journal, but that it rarely publishes articles on vegetation, perhaps giving him the impression that my entire field is unprestigious? Should he be provided with an explanation of the difference between prestige and usefulness, even though this may be perceived as making lame excuses for my failure to even

submit manuscripts to perhaps the most prestigious journal in my general academic area? None of these options is very attractive.

There are similar situations in other fields. *Ecology* would certainly be considered by any Dean as a prestigious outlet for any ecologist on his faculty. However articles in the field of physiological plant ecology are far more likely to be published in general purpose botanical journals (like *Bulletin of the Torrey Botanical Club*, *Botanical Gazette*, or *American Journal of Botany*) than in *Ecology*. In fact, one very productive physiological plant ecologist whom I know has even discontinued receiving *Ecology* and *Ecological Monographs* because he feels they are so unuseful in his research area. Yet, a Dean might consider a specialty journal like *Ecology* more prestigious than general journals like these three botanical ones, and one would be hard-pressed, without invoking the usefulness argument, to explain why one's publications, however numerous, were rarely in *Ecology*.

A few years ago a committee charged with interviewing candidates for our Arts and Sciences deanship was told by one candidate, already an associate dean of a major southern state university, "We don't just look at the publication list of a faculty member. We look up how often the publications are cited in *Science Citation Index*, and that tells us how significant the publications are." Under that system, the prestige of the journal in which the article appears is not so critical: what matters is how often other workers cite it.

While my students are frequently sent to *Science Citation Index* (SCI) to locate articles for their term papers or thesis research topics, we had not been using it as a mechanism to see whether work was "significant." The next day I stopped by the library to see how my work had fared. SCI did list some citations of articles I had authored or co-authored, but fewer than expected, and several citations I know about were not listed. Further investigation revealed that those citations of my articles did not show up in SCI because they had been cited in the botanical journal *Castanea*, a journal SCI does not cover.

Inquiry to SCI revealed why *Castanea* isn't covered: its "impact" is too low. "Impact" or "impact factor" is the ratio of the number of citations of articles from a journal during the most recent two years to the number of articles published in the journal during that two years (SCI 1987). It is an

attempt to measure the likelihood that articles in the journal will be cited by other researchers. A journal with a high impact factor is providing articles that other researchers feel a need to cite in their writing, so it clearly is useful to a large number of researchers. In fact, "impact" as measured by SCI is sometimes used as a means of determining prestige among journals. Numerical value of the impact factor for a given journal varies from year to year, and thus the journal's rank based on impact may vary also. For instance, *American Journal of Botany* had a higher impact factor in 1987 than *New Phytologist*, but in 1986 these were reversed; and in 1987 the *Bulletin of the Torrey Botanical Club* had a higher impact factor than *Botanical Gazette* while in 1986 the reverse was true (SCI 1986, 1987). However, if over a period of years a journal's impact factor is so low that SCI doesn't even include the journal in its coverage, then that journal is unlikely to be called "prestigious," and is probably not very useful either—or so one might think. *Capstan* is not alone in falling into this low impact category. Other journals used by field botanists, such as *Sida*, *Madroño*, *Southwestern Naturalist*, the long important systematics journal *Brittonia*, and even the venerable botanical journal *Rhodora* are likewise omitted from SCI's coverage because of their lack of "impact." Citation of one's work in articles published in these or other such (largely regional) journals will therefore not be picked up by SCI.

It should be noted that there is a time element in the calculation of the impact factor; cited articles more than two years old do not enter into the calculation. For convenience I will refer to this element as "quickness," related to how soon after publication articles are cited. On reflection, one would hardly expect a lot of "quickness" in journals in which the primary subject matter is field and museum or herbarium systematics or field ecology. It takes a long time to gather data in studies of this type, and such studies don't lend themselves to periodic progress report articles. Thus, when an article is ultimately published, it is unlikely to cite previously published progress reports of the just preceding years. Therefore, even if a newly published article inspires a researcher to start a related study, it will likely be more than two years before the second study is completed, written up, and shepherded through the review process to publication. By this time, citation of the first, initiating article is too late to count towards the impact

factor for the journal in which it was published. Field biology journals thus might be expected to have lower impact factors.

On the other hand, the data published in field, herbarium, and museum studies does not quickly become obsolete, so an article may be worthy of citation many years, and even decades, after the original publication. Thus, even if an article is rarely cited in the first two years after publication, this does not mean it is unimportant or lacking in significance, for other articles in which it will ultimately be cited in may still be years away from publication. The lag in "quickness" in systematics and field ecology studies may well be compensated for by long-time worth in articles in those disciplines.

The New Phytologist, trying in its advertising circular to persuade botanists to subscribe, reports that it has the "most favorable half-life" of broad-spectrum botanical journals. Half-life in this case refers to the median number of years since publication of the articles cited in the journal (SCI 1987). A short half-life would presumably mean that the authors publishing in that journal are keeping up on the very latest literature and cite mostly very recent articles. No doubt this is the point the editors of *The New Phytologist* had in mind. The other side of this, however, is that a short half-life may mean that in the fields covered by a journal, the information in articles more than a few years old is usually so out-moded that there is no reason to cite those articles. Such early obsolescence is not often the case in field biology studies. Therefore, journals which regularly publish articles on systematics or field ecology would be expected to show frequent citation of older articles, and thus a long half-life.

In the 12 papers I have authored or co-authored in this decade, 34 out of 173 entries in the "Literature Cited" were less than five years old at the time of citation. However, more than half the entries were more than 15 yr old when cited, and almost a quarter (22.5%) were over 30 yr old. The half-life of cited articles is greater than 15 yr, well beyond the ≥ 10 yr cutoff for "unfavorable" half-life of SCI. In contrast, the median half-life for all CSI citations is 6 yr, and less than 5% of the citations are older than 30 yr (CSI 1988). In my articles older entries were cited not because of unfamiliarity with more recent work, but because, despite passage of years, the information in the older articles was still pertinent to the studies

being done. Is a long half-life "unfavorable" in this case? Probably not.

No matter what its prestige or impact to other parts of the biological research community, a journal is *useful* to the individual researcher only if it regularly publishes articles which help that researcher keep up with the latest developments in his or her specialized field. There are, for instance, certain journals of which I have chosen to receive personal copies (by becoming a member of the professional societies which publish them). I want my own copies of those of those journals because any issue is likely to contain articles pertinent to my research and teaching. Other journals which may, from time to time (but not regularly), contain articles pertinent to my research I generally choose not to subscribe to. Rather, I depend upon occasional examination of the copies in the University library to keep up any articles in my research field published in those journals. Interestingly, many of the journals I choose to receive, because they are most useful to my research, are not high impact journals. Prestige as measured by SCI's impact figure does not necessarily coincide with *usefulness* as I have judged it in selecting which journals to receive.

In an effort to get some quantitative measure of which journals have been most useful in my research, frequency of citation of various journals in the 12 papers of mine mentioned earlier were examined (Table 1). While *Ecological Monographs* and *Ecology* are high impact journals by SCI's measurement, the third most frequently cited journal is one with such low impact that SCI doesn't even cover it, and this is also true of the sixth and seventh journals. In contrast, the prestigious (higher impact) botanical journals *American Journal of Botany* and *Botanical Gazette* and such prestigious European ecological journals as *Oecologia*, *Oikos*, and *Journal of Ecology* did not make my list. There was not a single citation from any of those five journals. This of course does not mean that these journals are not useful to me. I consult all of them regularly, and even receive a personal copy of *American Journal of Botany*. Still, there clearly is not a good correlation between SCI's "impact" in botany or ecology as a whole and usefulness as measured by citation in my published research.

The sample on which Table 1 is based is very biased, since 11 of the 12 papers dealt with forest vegetation. The remaining article dealt with the other area of plant ecology in which I do research,

TABLE 1. Sources of articles cited in twelve articles authored or co-authored by S. Ware 1980-1989 (journal citations only; books, theses, documents excluded). An asterisk means the journal is not covered by SCI.

Scientific journal (N=21)	Number of times cited (N=116)
Ecology	23
Ecological Monographs	19
*Castanea	15
Bulletin of the Torrey Botanical Club	14
American Midland Naturalist	12
*Virginia J. of Science	7
*J. Elisha Mitchell Scientific Society	4
*Jeffersonia	3
Vegatatio	3
American Naturalist	2
*ASB Bulletin	2
J. Forestry	2
*Rhodora	2
8 others, each	1

rock outcrop ecology. To get a view of what the most useful journals might be in that research area, the sources of literature cited in a recent review chapter (Baskin and Baskin 1985) dealing with autecology of rock outcrop plants were examined (Table 2). The greater representation of *American Journal of Botany*, *Botanical Gazette*, and *Canadian Journal of Botany* in their cited literature, and the relatively lower representation of *Ecology* and *Ecological Monographs* than in Table 1 is consistent with the earlier suggestion that articles on physiological plant ecology are more likely to appear in one of the general purpose botanical journals than in these two ecological journals. In this case also, usefulness as measured by frequency of citation and impact as measured by SCI do not correlate well. Only two journals are cited more often than *American Midland Naturalist*, which has only a moderate SCI impact factor. The regional journal *Castanea* is cited as often as *American Journal of Botany*; the *Journal of the Tennessee Academy of Science* is cited as often as *Botanical Gazette*. *Science*, regarded by many as the most prestigious American journal, provided only one citation.

Journals are useful not just for the information they provide a researcher, but also for the

TABLE 2. Sources of articles cited in a review chapter on rock outcrop ecology by Baskin and Baskin (1985).

Scientific journal (N=36)	Number of times cited (N=89)
Bulletin of the Torrey Botanical Club	12
Ecology	7
American Midland Naturalist	5
Evolution	5
J. Ecology (British)	5
American J. of Botany	4
Botanical Gazette	4
Canadian J. of Botany	4
Castanea	4
J. Agricultural Research	4
J. Tennessee Academy of Science	4
Contributions of the Gray Herbarium	3
New Phytologist (British)	3
Oecologia	2
Weed Research	2
Ecological Monographs	1
Science	1
19 others, each	1

interested readership they provide for the researcher's writings. Now that almost all researchers have easy access to a photocopying machine, it is probable that a smaller percentage of biologists request reprints than was once the case. Still, if the number of reprint requests per article is any indication of the size of the interested readership, then *Castanea* (a low impact journal), *Bulletin of the Torrey Botanical Club* (intermediate impact) and *Ecology* (high impact) are of approximately equal usefulness in providing interested readers for my work.

Perhaps a better indication that a journal provides an interested readership is the more frequent citation of one's articles in that journal. If this is true, *Bulletin of the Torrey Botanical Club* and *Castanea* (in that order) are providing the best readership for my work, *American Midland Naturalist* is third, and *Ecology* and *Virginia Journal of Science* are competing for fourth.

Two years ago I underwent a periodic (six-year) re-evaluation, which is required of all tenured faculty in my department. The evaluation committee

(composed of five of my colleagues) decided my performance merited my continuance and they even gave me some mild praise for my "continuing contribution to scholarship." They commented, however, that too many of my publications were in regional journals. The implication was, of course, that however meritorious my "continuing contribution" was, it would be even more so if more of it were in national and international (read "more prestigious") journals. It was no false accusation that I had been publishing in regional journals. The journals published in most often are *Castanea* (6) *Bulletin of the Torrey Botanical Club* (5), *Virginia Journal of Science* (5) and *Ecology* (3). *Castanea* plainly states that it invites articles relating to the flora and vegetation of the southern Appalachians and the southeastern United States, because that is the field of interest of its readership. The *Virginia Journal of Science* has no stated geographical limitations on its subject matter, but in practice its content, like that of most state academy journals, is heavily weighted toward the field biology and field geology of that state.

Why publish so often in these regional journals? I have long been interested in the distribution, abundance, and phytosociology of vascular plants (particularly of forest trees) and in the environmental factors which control these. Climate, geology, topography and their interactions usually control the distribution and phytosociology of forest trees. Since climate, geology, and topography all vary from region to region, vegetation also varies from region to region. While certain general principles are applicable everywhere, the details of relative abundance and phytosociological relationship among species are often only valid for a given region. It is risky to extrapolate findings in one region to another region where the levels of the controlling factors are different. Thus, vegetation studies, like studies of flora and fauna tend to be regional in extent and applicability, at least at the level of detail, and that is why almost all vegetation, floristic, and faunistic studies have a geographical term in their titles. The most interested readership for such studies will usually be other field biologists in that general region. This is in fact the very reason for the existence and usefulness of regional journals like *Castanea*, *Southwestern Naturalist*, *Prairie Naturalist*, *Great Basin Naturalist*, *Madroño*, *Northwest Science*, and most state academy journals.

If a vegetation ecologist were reporting on the existence of a new plant community process, or a major geographical extension of a vegetation type, then this might well be of great enough interest to readers on a national scale to be published in *Ecology* or *Bulletin of the Torrey Botanical Club*. If it is the first modern detailed study of the vegetation of a large portion of a physiographic province or of a major disjunct outlier of a widespread vegetation type, perhaps *Bulletin of the Torrey Botanical Club* or *American Midland Naturalist* would be the journals of choice. If the study is of the differences between two different portions of the same physiographic province in the southeastern U.S., then one might send it to *Castanea*. If the research involves the comparison of relative abundances of certain tree species above and below the scarp of a Coastal Plain terrace, then the appropriate choice might be a state Academy of Science journal, such as *Journal of the Elisha Mitchell Scientific Society* (North Carolina). While it makes sense to publish in the most prestigious journal one can, the choice of the journal should be determined in large by where the interested readership is to be found.

For workers in research areas such as molecular biology or plant or animal physiology, there is no geographic constraint on applicability of the results. For them, publication in a state academy journal might be regarded as "invisible," in the sense that it will almost certainly be overlooked by other workers in their specialty. Because of the regional nature of so many vegetation, floristic and faunistic studies, the appropriate state academy journals are routinely consulted by most field biologists, and thus these journals are not as "invisible" as they are in other subdisciplines. Because of an interest in the ecology of limestone outcrop plants, I routinely consult the *Journal of the Tennessee Academy of Sciences*, where pertinent articles occur from time to time (Table 2). Apparently other field ecologists also consult such state journals, for three titles my students and I published in the *Virginia Journal of Science* have since been cited in books, and none of the three citing authors were from Virginia.

SCI doesn't regard some of the regional journals in which I publish as very prestigious, because they have low impact factors. A Dean who counts SCI citations will perhaps underestimate the significance of my work, for he will never know my work was cited in these journals, since they are not

covered by SCI. My departmental colleagues may not esteem sufficiently the work I publish in these journals, because they are merely regional. Yet, when one considers which journals (a) regularly have articles pertinent to my research, (b) are most likely to be cited in my articles, (c) are most likely to cite my articles, and (d) seem to have a readership likely to be interested in my research, then these regional journals rank right up along with

ones of broader geographic coverage like *Ecology* and *Bulletin of the Torrey Botanical Club*. Given the geographical distribution of the plant communities I find particularly interesting, regional journals are likely to remain useful to me as both a reader and a contributor, despite any lack of prestige, impact, or esteem from some of my colleagues outside of field biology. I guess I'm just a regional kind of guy.

Literature Cited

- Baskin, J. M. and C. C. Baskin. 1985. Life cycle ecology of annual plant species of cedar glades of southeastern United States, pp. 371-398. *In* J. White (ed). *The Population Structure of Vegetation*. Dr. W. Junk Publishers, Dordrecht, Netherlands
- SCI. 1986. *SCI Journal Citation Reports*. 1986. Annual, Vol. 19. Institute for Scientific Information, Inc., Philadelphia. 1518 p.
- SCI. 1987. *SCI Journal Citation Reports*. 1987. Annual, Vol. 19. Institute for Scientific Information, Inc., Philadelphia. 1497 p.
- SCI. 1988. *SCI Journal Citation Index 1988*. Guide. Institute for Scientific Information, Inc., Philadelphia. 132 p.

Book Review

Sagebrush Country: A Wildflower

Sanctuary. Ronald J Taylor. Mountain Press Publishing Company. \$12.00

In his book, *Sagebrush Country*, Ronald Taylor attempts to provide the reader with a better understanding and appreciation of vegetation in the sagebrush steppe, a land considered by many to be a "wasteland." This is achieved primarily by the use of color photographs and non-technical description of steppe wildflowers. *Sagebrush Country* was originally published in 1974 by Ronald Taylor and Rolf Valum as part of Touchstone Press's "Wildflower" series. This 1992 version published through Mountain Press has added introductory information on sagebrush steppe communities and much improved color photographs.

A fairly long introduction precedes individual species photographs and descriptions. This allows interested individuals to learn about sagebrush country. Taylor defines the range of sagebrush country as the sagebrush steppe and Great Basin sagebrush desert areas in parts of Oregon, Washington, California, Nevada, Idaho, Montana, Utah, Colorado and Wyoming. Sagebrush, in the broad sense, is considered to include *Artemisia* species as a group, but *A. tridentata* is given emphasis.

A section on vegetative zones describes an admittedly over-simplified classification of vegetation pattern within the sagebrush steppe. Six zones are recognized: standard-type, lithosol, sand (dune), talus, meadow and saline. Taylor appropriately notes that the distribution of species within these general zones varies from location to location. However, by referring to Appendix 2 which lists species by zone, this arrangement may be useful in species identification for those who are able to readily recognize one of the six zones.

A brief and generalized section on plant adaptations follows the zonal description. Adaptations are divided into three categories which are described in most desert flora field guides: drought tolerators, drought avoiders and drought evaders. Outstanding adaptations of individual species are presented where appropriate in the main body of the book.

The final two descriptive sections of the introductory material touch upon faunal components

of sagebrush country. One section deals with pollination strategies, while the other describes animals of the steppe. I particularly liked the idea of presenting the reader with the concept of coadaptation of insects and steppe plants. It answers the questions of "why" there is such a variety of colors, shapes, sizes and odors of sagebrush wildflowers. However, the discussion on steppe animals is very brief and does not relate to steppe vegetation, as one might expect.

The main body of the book provides a color photo and written description of characteristics and other pertinent information (e.g. the derivation of the Latin name) for approximately 200 species of plants; a relatively broad selection of common steppe wildflowers. Species are organized by families which are listed alphabetically and, therefore, require a knowledge of family characteristics. For those who lack that knowledge, a key to families is provided in Appendix 1. Unfamiliar terms can be clarified by referring to the descriptive illustrations and/or glossary which follows the appendices.

Nearly all the plants included are native species, but four "weed" species are pictured: cheatgrass (*Bromus tectorum*), diffuse (*Centaurea diffusa*), spotted knapweed (*C. maculosa*) and yellow starthistle (*C. solstitialis*). Their inclusion seems well justified, because these plants are becoming more and more common in steppe areas and, as with cheatgrass, may be naturalized.

For those who want only to quickly search through the pages to find an unknown wildflower, the organization may be somewhat awkward, because it necessitates that one become familiar with the book. However, this book is ideal for those who want to learn common steppe wildflowers but do not want technical detail. *Sagebrush Country* is more than an identification guide providing thought provoking information about the steppe and the well-adapted plants and animals that live there. Taylor's writing style is informative, as well as entertaining, and gives the reader an overall appreciation of a seemingly harsh and desolate region.

—Richy J. Harrod
Leavenworth Ranger District
600 Sherbourne
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Northwest Science

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An abstract, written in complete sentences and not exceeding 250 words, should precede every article. It should succinctly state the objectives, the experimental design, the principal observations, and conclusions of the paper. Authors are reminded of the diverse disciplines and readership served by the journal; with this in mind, the abstract should conclude with a sentence or two stating the broader significance of the paper.

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Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1990).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

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November 1993

Volume 67, Number 4

COASTAL MARSHES
IN ALASKA

NORTHWEST SCIENCE



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Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science*, is open to individuals for \$20 per year (\$10 per year for students). Institutional memberships, \$40 per year. Sustaining membership, \$35 per year for individuals and \$100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

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Editor of *Northwest Science*

David L. Peterson
Cooperative Park Studies Unit
University of Washington, AR-10
Seattle, Washington 98195

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Announcements

Annual Meeting of the Northwest Scientific Association

The 67th Annual Meeting of the Northwest Scientific Association will be held on March 24-26, 1994, at Central Washington University in Ellensburg, Washington. Other organizations are expected to participate in the meeting, including the Northwest Lichen Guild, Rare Plant Consortium, Society for Northwestern Vertebrate Biology, and the Association of Washington Geographers.

Three symposia have been proposed that are relevant to scientists and resource managers in the Pacific Northwest. These symposia will focus on: research in forest canopies, the Yakima River and associated resources, and the ecology and management of bull trout. The meeting will also have several sections for contributed papers. In addition, several field trips will be led by local scientists. Pat O'Hara, renowned wildlife and nature photographer, will be the guest speaker at the banquet, and give a presentation on the Beringian Heritage International Park.

All those interested in science and resource management issues in the Pacific Northwest are invited to attend. Students are especially encouraged to attend and participate in invited paper sessions. Special efforts will be made to reduce costs for student attendees. For information, registration materials, and abstract forms, please contact Dr. Bill Barker, Biology Department, Central Washington University, Ellensburg, WA 98926 (USA); telephone 509-963-2731; fax 509-963-1047. Deadline for submission of paper abstracts is February 1, 1994.

1994 Student Research Grant

I. ELIGIBILITY

Applicants must be regular members of the Northwest Scientific Association. *Northwest Science* (the journal of the society) has information for joining the society.

II. PREPARATION OF THE PROPOSAL

A cover page should be provided to include: Name and address of applicant, associated institution, name of major professor/advisor, degree program, year in school, and amount of money requested (maximum of \$500).

The proposal should include: Title, Statement of Justification, Methodology/Experimental Design (including methods of analysis), and detailed budget (on separate page).

The proposal length should be no more than three (3) *double spaced* pages (not including budget page).

Proposals are due on or before February 15, 1994 and should be sent to:

Dr. David H. Wagner
Department of Biology
University of Oregon
Eugene, OR 97401
Phone: (503) 346-3033

Grants will be awarded at the annual meeting of the Northwest Scientific Association held in Ellensburg, Washington, March 24-26, 1994.

Awards provided by the Northwest Scientific Association are designed to help students complete research projects in the basic and applied sciences and social sciences. Monies should be used only to support research activities of the student. It is expected that students will report results of their research at a future NSA meeting.

Vegetation of Coastal Marshes near Juneau, Alaska

Abstract

The purpose of this study was to demonstrate the relationship of physiography to the organization of southeast Alaskan coastal marsh vegetation. Distributions of species and vegetation units were analyzed in relation to marsh landform types in four Juneau-area coastal marshes. Eleven vegetation types were identified. Species composition of each vegetation type was not consistent within or among sampled marshes, but each vegetation type occurred consistently on a particular combination of landforms. These conditions seem to be the result of individualistic species behavior in habitats with inconstant, non-linear environmental gradients arising from site-specific combinations of physiographic processes. The marshes were compared and classified in terms of landforms and physiographic characteristics of associated vegetation types, that is, the habitat-vegetation complex. The complexes occurring in the Juneau area were tidal silt sedge and sedge-grass marsh; tidal sand *Salicornia* marsh; tide-influenced grass meadow; *Elymus arenarius* upper marsh border and drift line; prostrate and scrambling forbs and rhizomatous grasses of upper beaches and sand spits; coastal forb meadow on drift lines and above marsh borders; fresh sedge-forb marsh; and emergent forbs of marsh ponds. Classification in terms of habitat-vegetation complexes makes possible comparison of Juneau-area marshes with other marshes of different vegetation-type composition in southeast Alaska.

Introduction

Coastal marshes seem to be a relatively simple habitat (Bertness and Ellison 1987) with a common general hydrologic regime, the tides, creating a common set of physical parameters to which coastal marsh plants must adjust. Therefore, one could reasonably expect to identify some unifying characteristics of coastal marsh vegetation. Nevertheless, attempts to characterize marsh vegetation on the North American west coast (Macdonald and Barbour 1974; Macdonald 1977a,b; see Stone 1984 for additional references) make clear how much marshes differ from place to place. In Alaska the problem of identifying common characteristics is further complicated by gradients of physical parameters apparently oriented in different directions (e.g., seaward, landward, and transverse) (Batten *et al.* 1976), making it difficult with available analytical techniques to sort out the effects on plants of individual physical characteristics of coastal marsh habitats.

A physiographic approach (e.g., Miller and Egler 1950) avoids these problems by viewing species and vegetation in relation to types of coastal marsh landforms rather than to numerical values of physical parameters. Landforms integrate particular combinations of physical conditions (Hack and Goodlett 1960). Therefore, inferences (*sensu* Egler 1977) may be drawn about species and vegetation behavior in relation to physical characteristics of habitat even though gradients of individual

parameters may be non-linear, multi-directional and not progressive. Reconnaissance of coastal marsh vegetation near Juneau, Alaska, indicated both non-linear, non-progressive behavior of physical gradients and inconsistent relationship of plant species and vegetation types to identifiable physical gradients. The purpose of this study, which was part of a larger project (Stone 1984), was to demonstrate the influence of physiography on the organization of coastal marsh vegetation in this area by describing species distributions and vegetation patterns in relation to landform types.

Methods

Study Area

The four coastal marshes studied (Table 1) encompass the widest variety of combinations of marsh physiography and vegetation types readily accessible in the Juneau area but still predominantly influenced by natural processes. The sites are within 50 km of Juneau, Alaska (58°18'0"N, 134°25'0"W) (Figure 1), a recently glaciated area of mild climate (for its latitude), high rainfall (140 to 234 cm), and structurally weak bedrock of high relief. Like most other coastal marshes, these sites are subject to the physiographic/hydrologic influences of coastal storms, river flooding, and freshwater seepage. However, other physiographic influences are, in combination, unique to southeast Alaskan marshes. Large sediment loads and large summer discharges of glacial rivers produce a greater rate of sediment deposition and a greater degree of freshwater dilution than in other North American coastal marshes. High tides, floods, and

¹Present address: Science Dept., Edith Cowan University, Joondalup, WA 6027, Australia

TABLE 1. Physical characteristics of coastal marshes sampled in the Juneau area.

	Mendenhall River	Lemon/Switzer Creek	Eagle River	Gastineau Channel
distance (km) and direction from Juneau	12 NW	8.3 N	32 NW	6.4 S
area (ha)	415	65	140 ^a	0.4
marsh landscape	glacial river delta	creek delta over glacial valley fill	glacial river delta	wave-carved pocket in rock fill
surrounding landscape	valley walls	valley walls	sand spits	rockfill terrace
exposure to sea	sheltered by peninsulas	sheltered by peninsula and valley wall	exposed on 3 sides	exposed on 1 side
substrate	silt	silt	sand, silt ^a	thin sand, gravel and silt over rock fill
sediment source	glacial meltwater	tidewater	glacial meltwater	tidewater
tidewater salinity ^b	brackish	brackish	saline, brackish ^a	brackish

^atwo marshes^bafter Federal Water Pollution Control Administration (1966)

storms bring in drift logs, and cold air drainage off the icefields in winter generates particularly violent (to 300 km/hr) dry wind storms. The tide range is unusually large (≈ 6.3 m), and tidal influence reaches far inland in flat areas.

Data Collection

Neither established benchmarks nor tidal data recording stations were near enough to the marshes for use as valid reference points. Therefore, relative elevation was used to define landforms. Sampling transects, made in June and August, 1981, were of two kinds: measured (by hand-held compass, hand level, stadia rod, and pacing) and estimated (by marking sample locations on USGS 15-minute topographic maps and eye estimate of plot size). Positions and lengths of transect lines were chosen to cross all physiographic site types in a marsh. Physiographic site types were identified in the field by visually recognizable surface form, by breaks in slope, and by changes in degree and direction of slope (Small 1970, p. 6). Where a single transect could not be laid out to cross all types, additional transects were made. Sampling was extended beyond marsh borders in three of the four marshes. Measured sample plot size was 6 x 6 ft (1.8 x 1.8 m), an area consistent with the ground area sampled at points on estimated transects.

In each physiographic category encountered along the transect, one sample plot was placed in each homogeneous patch of vegetation. Thus, the

number of plots in each physiographic category at a given sample site depended on the number of vegetation types in the physiographic category and the number of times the category was crossed by the transect(s). Altogether 106 plots were sampled: 38 in the Eagle River sand marsh, 26 in the Eagle River silt marsh, 24 in the Gastineau Channel marsh, 15 in the Lemon Creek-Switzer Creek marsh, and three in the Mendenhall River marsh (upper part only was sampled). Totals for each physiographic category are given in Table 2. (The term "marsh," where unqualified, refers to sand and silt marshes together.)

For each sample plot, relative elevation, landform type (site categories of Table 2), and surface sediment texture (silt, sand, or gravel—determined by eye) were recorded. The identity of each vascular plant species present was also recorded, and species were listed as primary (meaning visually dominant) or secondary (not visually dominant). Plants not identifiable in the field were collected for identification, and a voucher specimen was taken of each vascular plant species found at the sample sites. Hultén (1968) was the nomenclatural authority.

Data Analysis

Four kinds of analysis were made from the data for each sample plot: physiographic classification of the site, physiographic classification of species (species distributions among the physiographic site

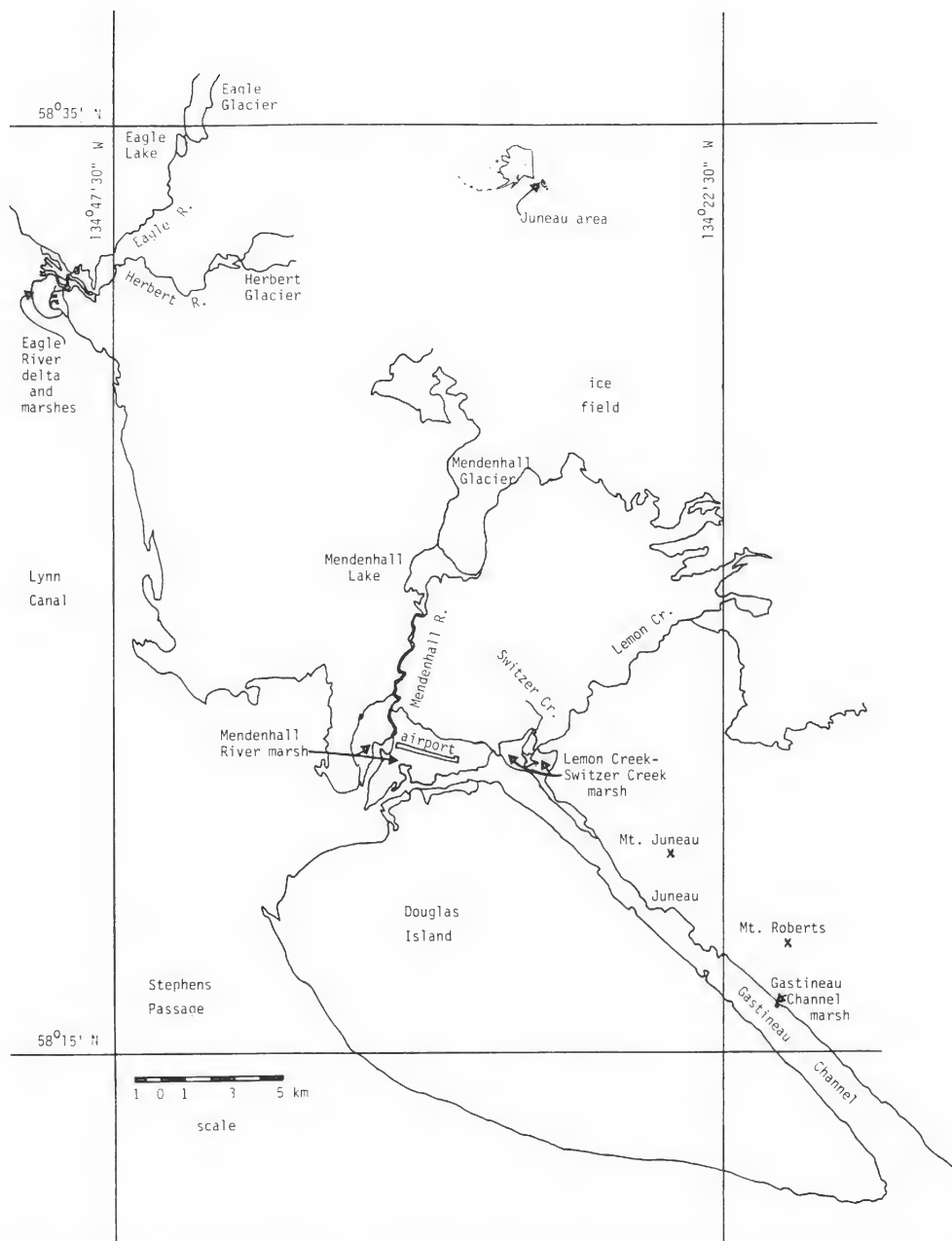


Figure 1. Juneau area, showing locations of sampled marshes. Glaciers and watercourses shown in positions as on source maps (USGS topographic series 1:63,360 Juneau A-1, B-1, B-2, B-3, and C-3, published 1948-1962, minor revisions 1966-1975). Inset: Location of Juneau area in Alaska.

TABLE 2. Landforms and physiographic categories of Juneau area coastal marshes.

Landform	Physiographic site category	Figure no. where illustrated	Number of sample points in category	Surface shape
marsh sites	lower marsh border	2c,d	6	straight or concave
	tidal marsh—sand	2c,d	26	straight (no levee)
	tidal marsh—silt	2b,c,d	27	concave with levee, straight without levee
	channel bank	2a,b	4	convex
	small channel	2a-c	2 ^a	concave
	tide-influenced meadow	2d	1	straight
upper marsh border sites	upper marsh border	2a,c,d	14	concave
	drift line	2a-d	6	convex
beach and foreshore	beach	2a,d	3	straight or concave
slopes above marsh border	front spit slope	2a,d	2	straight
	back spit slope	2a,c,d	6	straight
	seepage slope	2b,c	2	straight
	fill slope	2c	2	straight
upland	spit top	2a,d	3	convex
extratidal wet sites	fresh marsh	2b	2	straight or concave
	marsh pond	2b	2	concave
Total sample points			106	

^acombined in Table 5 with tidal silt marsh sites

categories of Table 2), vegetation-type classification of species, and physiographic classification of vegetation types. These analyses made it possible to elucidate the spatial arrangement of marsh landforms and the relationships of species and vegetation types to them (Zimmermann and Thom 1982).

The physiographic site types identified in the field were grouped in categories based on cross-sectional geometry in marsh elevation profiles (Small 1970). Cross-sectional form was combined with recorded qualitative field observations of moisture/tidal flooding regime and surface substrate composition to produce the physiographic site categories. Such landform analysis is standard procedure in geomorphology and physiographic ecology for definition and identification of physiographic features of habitat at the scale of the present study (Raup 1975, Semeniuk *et al.* 1989).

Classification of vegetation types of the 106 sample plots, based on species composition, was

done by the Braun-Blanquet method (Mueller-Dombois and Ellenberg 1974). The first segregation defined groups with no overlap in distinguishing species. Some of these groups contained locationally distinct subgroups and so were separated into two vegetation types. Vegetation types were named either for the primary species if there were only one or two, or for the physiognomic type (*sensu* Raup 1975, p. 159) (*e.g.*, grasses, forbs) of the several primary species.

Physiographic classifications of species and vegetation types were based on tabulations of species- and vegetation-type occurrences for each physiographic site type. A species or vegetation type was considered characteristic of a site category if it occurred in one third or more of all sites in a site category or only in that category, or if one fourth or more of the total sample sites for a species or vegetation type occurred in that site category (a procedure modified from Raup 1969).

Results and Discussion

Physiographic Classification of Sites

The six types of landforms of the Juneau-area coastal marshes and their subdivisions into physiographic site categories are shown in Table 2 and Figure 2. The shape, slope angle, position, and composition of these surfaces determine their hydrologic characteristics (Hack and Goodlett 1960), which are essential components of habitat in the sampled marshes. Concave surfaces collect water and so are flooded or saturated more frequently and/or longer than surfaces with other shapes. Convex surfaces shed water and thus are drier and flooded less often and for shorter periods than surfaces of other shapes. The straight surfaces have intermediate hydrologic conditions. The steeper slopes of levees and of landforms above marsh borders shed water faster than the imperceptibly sloping marsh and tide-influenced meadow surfaces.

Drift lines (Table 2, Figure 2) are created by logs left by storm tides. Sediment collects around the logs, slightly raising the ground surface above the surrounding landscape and thus increasing the drainage.

The differences in position and substrate composition of slopes in all site categories (Table 2, Figure 2) also produce different hydrologic conditions (Table 1) and thus are important components of habitat in the sampled marshes. Marsh sites occur at the lowest elevations and thus have the longest and most frequent tide coverage. Within these landforms, channel banks and lower marsh borders experience the highest current velocities as well as the longest tidal flooding periods. Tide-influenced meadows are flooded or partly flooded by the higher of the semi-diurnal mixed tides. Beaches and upper marsh borders are flooded by storm tides and higher spring tides. Because of their position facing the sea, beaches receive beating by waves, whereas marshes and upper marsh borders are more sheltered.

The position of the tidal inlet channel also affects hydrologic conditions in marshes. At sites where the channel opens directly into the ocean, entering tidewater is clear and undiluted by fresh water, and marsh floors have substrates coarser than silt (Table 1). These marshes are well drained and well aerated. At sites where the tidal channel opens into a river channel or the tidewater spreads over flats at a river mouth, the water flooding the

marshes is brackish, silty, tidally dammed river water. The floors of these marshes are silt (Table 1), less well drained and less well aerated than coarser substrated marshes.

Substrate composition, another basic component of habitat, influences the drainage characteristics of marshes, slopes above marsh borders, and uplands. Sand marshes are better drained than silt marshes. Sand spits are well-drained, whereas the bedrock (seepage and fill) slopes and hillsides of valley walls are impermeable under generally wet soils through which fresh water seeps into upper marsh borders, tide-influenced meadows, extratidal wet sites and upper parts of marshes (Figure 2).

The relationship of the upper marsh border to other site categories depends on the arrangement of landforms. The upper marsh border may occur at the upper edge of marsh (Figure 2a), within or above tide-influenced meadow (Figure 2d), or beside a tidal channel at the base of a spit. On gentle slopes above tidal marsh, the upper marsh border grades into or interfingers with the landforms of tide-influenced meadow and slopes above marsh borders. The variety of possible arrangements of landforms and the shape, slope angle, topographic position, and substrate composition of landforms determine the seaward-to-landward sequence of vegetation types (see "Habitat-Vegetation Complexes of Juneau-Area Coastal Marshes" below).

Physiographic Classification of Species

Based on their occurrence in the physiographic site types of Table 2, plant species can be grouped into five categories: tidal marsh species (on lower marsh borders, sand marshes, silt marshes, and channel banks), species of tide-influenced sites (on tide-influenced meadows, upper marsh borders, drift lines, and beaches), species of slopes above marsh borders (on spit slopes, seepage slopes, and fill slopes), upland species (on spit tops), and species of extratidal wet sites (in fresh marshes and marsh ponds) (Table 3). Within this classification species vary in their range of occurrence. On the coastal marsh and tide-influenced sites, 13 of the 14 primary species and two of the five secondary species were found on more than one site type. Above the upper marsh border, 21 of the 30 species occurred on more than one site type. This variability makes it difficult to use species distributions alone to identify common characteristics among coastal marshes of the Juneau area.

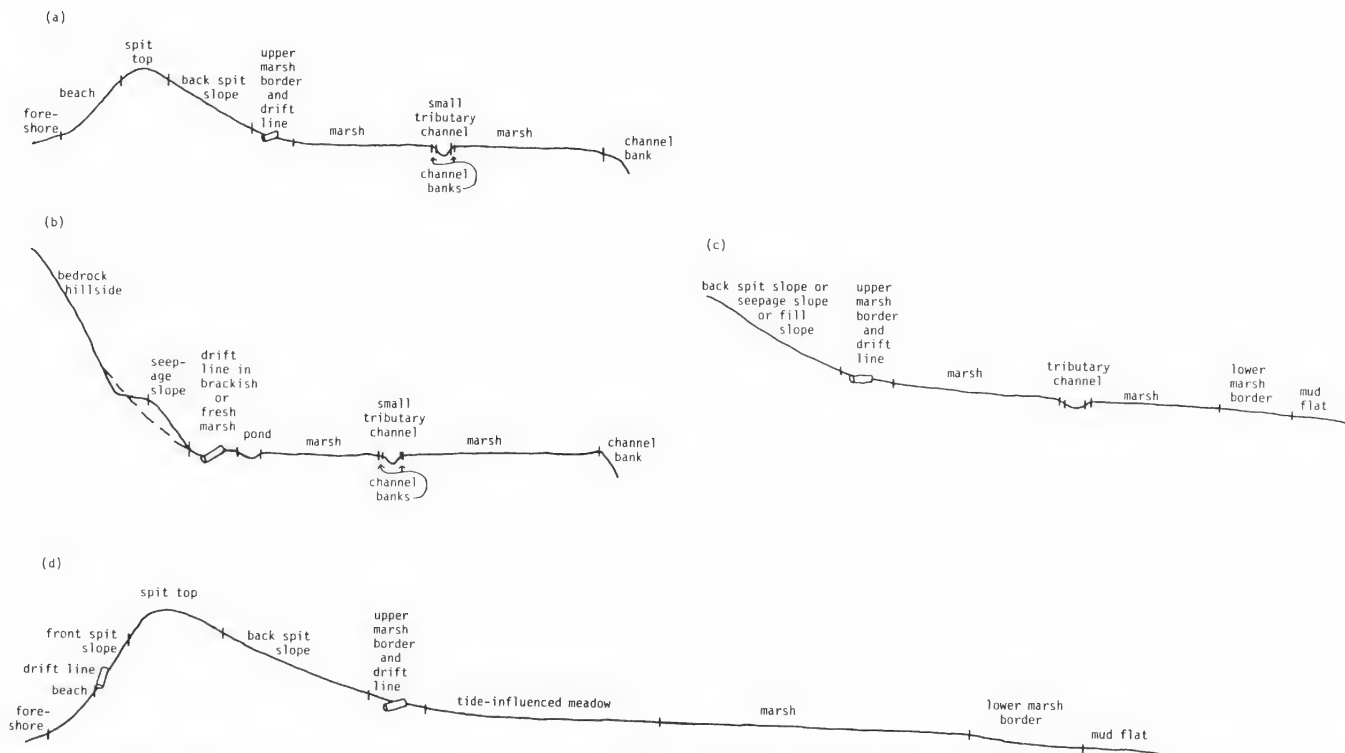


Figure 2. Generalized landforms of Juneau area coastal marshes illustrating the variety of combinations in the study area. (a) cross-section of marsh without tide-influenced meadow and with slight downward slope toward sand spit; (b) cross-section of marsh with natural levee (at channel bank) and ponds; (c) longitudinal profile of marsh without tide-influenced meadow; (d) longitudinal profile of marsh with tide-influenced meadow and sand spit. Dashed line in (c) shows the former natural slope and solid line in the same area is the present cut-and-fill slope. Vertical scales exaggerated; horizontal scales not constant.

TABLE 3. Plant species occurrence by physiographic site category.

Plant species	Site Category	marsh sites					upper marsh border sites	beach	slopes above marsh border				upland	extratidal wet sites		
		lower marsh border	sand marsh	silt marsh	channel bank	tide-influenced meadow	upper marsh border	drift line	beach	front spit slope	back spit slope	seepage slope	fill slope	spit top	fresh marsh	marsh pond
Tidal marsh species group																
<i>Puccinellia nutkaensis</i>		pri ^a	pri	pri	pri											
<i>Spergularia canadensis</i>		pri	sec	sec												
<i>Carex lyngbyaei</i>		pri		pri	pri										pri	
<i>Triglochin maritimum</i>		pri	sec	sec												
<i>Fucus</i> sp.		pri	sec													
<i>Salicornia virginica</i>			pri													
<i>Plantago maritima</i>			pri	sec												
<i>Suaeda maritima</i>			sec													
<i>Glaux maritima</i>			s/p ^b	sec												
<i>Stellaria humifusa</i>			sec	sec	sec											
<i>Cochlearia officinalis</i>			sec													
<i>Atriplex gmelini</i>			sec	sec												
<i>Hordeum jubatum</i>			sec			pri										
<i>Eleocharis kamschatica</i>				sec												
<i>Potentilla pacifica</i>				p/s ^c		pri										
Tide-influenced species group																
<i>Festuca rubra</i>						pri				p/s	sec		pri	pri		
<i>Deschampsia caespitosa</i>						pri					s/p	sec	pri			
<i>Elymus arenarius</i>						pri	pri	pri	pri	pri	pri	pri		pri		
<i>Honckenya peploides</i>							pri		pri	pri	pri			pri		
<i>Lathyrus maritimus</i>								pri	pri	pri	p/s	pri		pri		
Slopes-above-marsh-border species group																
<i>Achillea millefolium</i>							pri			pri	sec	pri	pri	pri		
<i>Hordeum brachyantherum</i>											sec	sec	sec			
<i>Angelica lucida</i>										pri	s/p	pri		pri		
<i>Mertensia maritima</i>											sec			pri		
<i>Lupinus nootkatensis</i>										pri	sec	sec		pri		
<i>Castilleja unalaschensis</i>											sec			pri		
<i>Heracleum lanatum</i>										pri	sec	pri		pri		
<i>Ligusticum scoticum</i>										pri	p/s	sec		pri		
<i>Conioselinum chinense</i>										pri	p/s			pri		
<i>Galium trifidum</i>											sec			sec	sec	
<i>Malus fusca</i>											sec			sec		
<i>Maianthemum dilatatum</i>											sec					
<i>Sagina crassicaulis</i>											sec					
<i>Actaea rubra</i>											sec					
<i>Epilobium angustifolium</i>											pri					
<i>Oenanthe sarmentosa</i>												pri			pri	
<i>Melilotus alba</i>													pri			

continued next page

TABLE 3 (Continued). Plant species occurrence by physiographic site category.

Plant species	Site Category	marsh sites					upper marsh border sites	beach	slopes above marsh border				upland	extratidal wet sites		
		lower marsh border	sand marsh	silt marsh	channel bank	tide-influenced meadow	upper marsh border	drift line	beach	front spit slope	back spit slope	seepage slope	fill slope	spit top	fresh marsh	marsh pond
Upland species group																
<i>Equisetum arvense</i>														sec		
<i>Carex macloviana</i>														sec		
<i>Fritillaria camchaticensis</i>														pri		
<i>Rubus arcticus</i>														sec		
<i>Trientalis europaea</i>														sec		
Extratidal wet site species group																
<i>Parnassia palustris</i>															sec	
<i>Caltha palustris</i>															sec	
<i>Potentilla palustris</i>															sec	
<i>Myrica gale</i>															sec	
<i>Cicuta douglasii</i>															sec	
<i>Chrysanthemum arcticum</i>															sec	
<i>Hippuris tetraphylla</i>																pri

^apri = visual aspect dominant, sec = all other species (see "Data Collection" in text)

^boccurs as sec more often than as pri

^coccurs as pri and sec with approximately equal frequency

Vegetation-Type Classification of Species

The eleven vegetation types identified from Braun-Blanquet analysis are named for their constant primary species or physiognomic types (Table 4). Their occurrences in the sampled marshes are shown in Figure 3.

Although each vegetation type is distinguished by a unique set of primary species, many species occur in more than one vegetation type (Table 4). In the coastal marsh and tide-influenced vegetation types, 12 of the 14 primary species and three of the five secondary species occur in more than one type. Above the upper marsh border, nine of the 28 species occur in more than one vegetation type (two of the 30 species referred to in the preceding section occurred too infrequently to be classified in the Braun-Blanquet analysis). Furthermore, the vegetation types vary in species composition within and among marshes. This variability is quite evident in the tables produced for the Braun-

Blanquet analysis (Table 13 in Stone 1984) and is generally related to microhabitat differences within vegetation types.

Physiographic Classification of Vegetation Types

Table 5 shows the association of vegetation types with the physiographic site categories of Table 2. Each vegetation type occurs consistently on one physiographic site category or a few to several topographically related categories, such as marsh, lower marsh border, and channel bank; tide-influenced meadow and certain slopes above marsh borders; or categories usually above tidal influence. Figure 3 shows the spatial relations among vegetation types at the study sites. Notice that each marsh has a unique combination of vegetation types occurring in a unique sequence along a gradient inland, which makes similarities among marshes difficult to identify.

TABLE 4. Plant species occurrence by vegetation type.

Plant species	Vegetation type ^a									
	cm				ti		aumb	ti	aumb	
	<i>Salicornia virginica</i>	<i>Puccinellia-Plantago</i>	<i>Puccinellia-Carex</i>	<i>Carex lyngbyaei</i>	<i>Elymus arenarius</i>	<i>Honckenya peploides</i>	<i>Elymus-Lathyrus</i>	coastal grass meadow	coastal forb meadow	fresh <i>Carex</i> marsh <i>Hippuris tetraphylla</i>
<i>Salicornia virginica</i>	pri ^b									
<i>Puccinellia nutkaensis</i>		pri	pri							
<i>Plantago maritima</i>		pri	sec							
<i>Suaeda maritima</i>		sec								
<i>Glaux maritima</i>		pri	sec	sec						
<i>Potentilla pacifica</i>		sec		p/s ^c	pri					pri
<i>Spergularia canadensis</i>		pri	sec	sec						
<i>Triglochin maritimum</i>		sec	p/s	sec						
<i>Stellaria humifusa</i>		sec	sec	sec						
<i>Cochlearia officinalis</i>		sec	sec							
<i>Hordeum jubatum</i>		sec						pri		
<i>Fucus</i> sp.		pri								
<i>Atriplex gmelini</i>		sec	sec							
<i>Carex lyngbyaei</i>			pri	pri						pri
<i>Elymus arenarius</i>					pri		pri		pri	
<i>Honckenya peploides</i>					pri	pri	pri			
<i>Lathyrus maritimus</i>							pri		pri	
<i>Mertensia maritima</i>							pri			
<i>Festuca rubra</i>								pri	pri	
<i>Hordeum brachyantherum</i>								sec		
<i>Deschampsia caespitosa</i>								pri		sec
<i>Achillea millefolium</i>									pri	
<i>Lupinus nootkatensis</i>									pri	
<i>Heracleum lanatum</i>									pri	
<i>Angelica lucida</i>									pri	
<i>Ligusticum scoticum</i>									pri	
<i>Conioselinum chinense</i>									pri	
<i>Castilleja unalaschensis</i>									pri	
<i>Galium trifidum</i>									sec	sec
<i>Epilobium angustifolium</i>									pri	
<i>Malus fusca</i>									sec	
<i>Oenanthe sarmentosa</i>									sec	sec
<i>Actaea rubra</i>									sec	
<i>Polygonum viviparum</i>									sec	
<i>Maianthemum dilatatum</i>									sec	
<i>Fritillaria camchatcensis</i>									pri	
<i>Rubus arcticus</i>									sec	
<i>Sagina crassicaulis</i>									sec	
<i>Trientalis europaea</i>									sec	
<i>Carex macloviana</i>									sec	
<i>Parnassia palustris</i>										sec

Continued, next page

TABLE 4 (Continued). Plant species occurrence by vegetation type.

	cm				Vegetation type ^a				aumb		
	<i>Salicornia virginica</i>	<i>Puccinellia-Plantago</i>	<i>Puccinellia-Carex</i>	<i>Carex lyngbyaei</i>	<i>Elymus arenarius</i>	<i>Honckenya peploides</i>	<i>Elymus-lathyrus</i>	coastal grass meadow	coastal forb meadow	fresh <i>Carex</i> marsh	<i>Hippuris tetraphylla</i>
Plant species											
<i>Myrica gale</i>										sec	
<i>Caltha palustris</i>										sec	
<i>Potentilla palustris</i>										sec	
<i>Cicuta douglasii</i>										sec	
<i>Chrysanthemum arcticum</i>										sec	
<i>Hippuris tetraphylla</i>											pri

^acm = coastal marsh vegetation type, ti = tide-influenced, aumb = above upper marsh border

^bpri = visual aspect dominant, sec = all other species (see "Data Collection" in text)

^coccurs as pri and sec with approximately equal frequency

Habitat-Vegetation Complexes of Juneau-Area Coastal Marshes

Given the marsh-to-marsh differences in vegetation-type composition and arrangement on a sea-to-inland gradient in the Juneau area (Figure 3), comparing the marshes in terms of community composition (the usual approach - *e. g.*, Watson 1981) would seem inadequate. Raup's (1975, p. 130) concept of the habitat-vegetation complex could be used in this situation. Raup described the shoreline vegetation of lakes in the Athabasca-Great Slave Lake region in terms of "form types" and recognized 10 types that, because they occupied sites of different "moisture regime, substrate, or topographic position," were called "habitat-vegetation complexes." These complexes are combinations of physiographic site characteristics with a physiognomic characterization of the vegetation, *e.g.*, "aquatic habitats with submerged and/or emergent plants" and "herbs and low or trailing shrubs on middle beaches of large lakes."

Raup (pers. comm.) originally intended his concept to be used only in certain situations where he has worked. I believe that it is also applicable to an understanding of southeast Alaskan coastal marsh vegetation patterns, because it frees us from

the restricted possibilities for comparison imposed by the use of communities, whose definition requires particular species compositions. It also allows meaningful comparisons of vegetation in groups of marshes with unique sets and spatial arrangements of vegetation types by providing a vegetational component (a physiognomic type) integrated with environmental parameters in physiography (as in Hack and Goodlett 1960).

Habitat-vegetation complexes for coastal marshes of the Juneau area can be derived by generalizing from the physiographic classification of vegetation types of Table 5. Each complex is distinguished by a unique physiographic site category (Table 2) or combination of categories occupied by a physiognomically distinct vegetation type (Table 4) or set of vegetation types as described below. Nine habitat-vegetation complexes are recognized here for Juneau-area coastal marsh systems. (The unique distinguishing feature of each complex is underlined.)

The habitat-vegetation complexes of the marshes and their immediate surroundings are:

- 1) tidal sedge and sedge-grass marshes on silt substrate;
- 2) tidal grass-forb marshes on substrate coarser than silt;

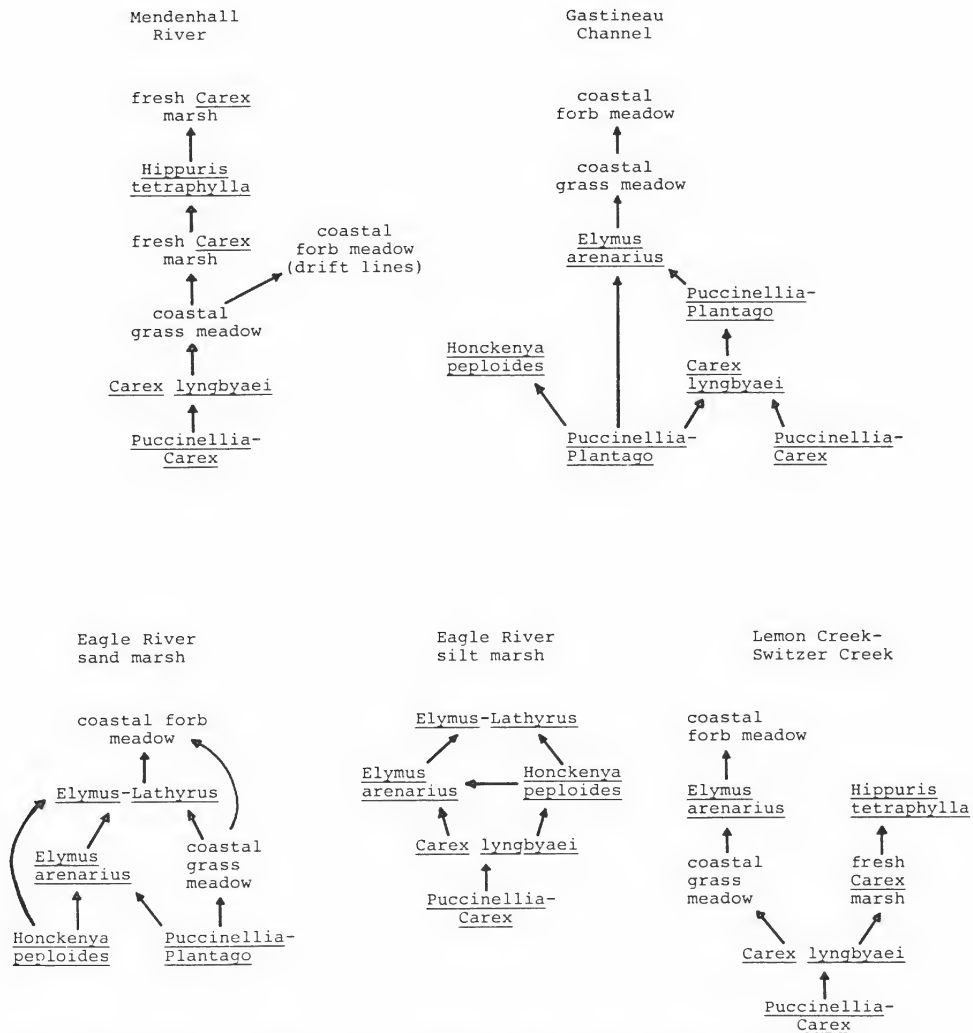


Figure 3. Spatial arrangement of vegetation types in Juneau-area coastal marshes. Arrows point inland.

- 3) succulent vegetation of tidal sand marshes;
- 4) graminaceous vegetation of tide-influenced meadows;
- 5) Elymus arenarius vegetation type of upper marsh borders and drift lines;
- 6) prostrate and scrambling forb and rhizomatous grass vegetation of upper beaches and sand spits;
- 7) coastal forb meadow vegetation of sand spits, slopes above marsh borders, and drift lines;

- 8) sedge-forb vegetation of fresh marshes inland of usual tidal influence or recently elevated above tidal influence;
- 9) emergent vegetation of apparently brackish marsh ponds in tidal and recently tidal marshes.

Complexes 1 and 2 include small channels, channel banks, and lower marsh borders as marsh sites, because the vegetation of these sites is physiognomically similar within each complex on

TABLE 5. Physiographic classification of vegetation types (x = vegetation type characteristic of the indicated site categories).

Physiographic Category	marsh sites					upper marsh border sites	beach	slopes above marsh border				upland	extratidal wet sites		
	lower marsh border	sand marsh	silt marsh	channel bank	tide-influenced meadow	upper marsh border	drift line	beach	front spit slope	back spit slope	seepage slope	fill slope	spit top	fresh marsh	marsh pond
Vegetation Type															
<i>Salicornia virginica</i>		x													
<i>Puccinellia-Plantago</i>	x	x													
<i>Puccinellia-Carex</i>	x		x	x											
<i>Carex lyngbyaei</i>			x												
coastal grass meadow					x		x			x		x			
<i>Elymus arenarius</i>						x	x								
<i>Honckenya peploides</i>								x							
<i>Elymus-Lathyrus</i>							x		x	x			x		
coastal forb meadow							x		x	x	x	x	x		
fresh <i>Carex</i> marsh														x	
<i>Hippuris tetraphylla</i>															x

these site categories. Complex 1 also combines two vegetation types, *Puccinellia-Carex* and Lyngbye sedge (*Carex lyngbyaei*) because their habitat behaves as a single unit. Complex 3 is included tentatively, since it is known from only one site. It is distinguished from complex 2 by its succulent vegetation type and its isolated occurrence. Complex 5 combines all site categories with the lyme grass (*Elymus arenarius*) vegetation type; complex 6 all site categories with the seabeach sandwort (*Honckenya peploides*) and *Elymus-Lathyrus* types. Complex 7 includes all the kinds of physiographic sites with coastal forb meadow vegetation. The other complexes are self-explanatory with reference to the list above and to Table 5.

Five habitat-vegetation complexes are associated with marshes; the others occur on landforms surrounding the marshes (Tables 2 and 5). The complexes are intended to describe the vegetation and landscape of the sampled marshes so as to identify their similarities; they are considered not necessarily definitive for a larger area.

The relationship of vegetation type to landform in the habitat-vegetation complex can be used to explain major aspects of the differences in species

and vegetation-type composition among the sampled marshes of the Juneau area. Because a particular vegetation type is associated with only one or a few kinds of landforms, it will be present in a marsh only if its associated landform(s) is(are) present. The spatial relationship of landforms in a marsh will determine the spatial relationship of vegetation types and thus account for the differences in the spatial sequence of vegetation types among marshes shown in Figure 3.

For example, where the substrate is coarser than silt, the *Puccinellia-Plantago* vegetation type occurs over the whole tidal sand marsh site category. This explains why *Puccinellia-Plantago* is the only marsh vegetation type in the Eagle River sand marsh. Where the marsh floor is silt, there are two marsh vegetation types: *Puccinellia-Carex* always occurs below *Carex lyngbyaei* in elevation. Three marshes in the Juneau area have this sequence: Mendenhall River, Lemon Creek, and Eagle River silt marsh. The Gastineau Channel marsh has both the *Puccinellia-Carex* to *Carex lyngbyaei* sequence and the *Puccinellia-Plantago* vegetation type, because it has a small area covered with silt surrounded by a sand and gravel surface (Table 1).

Immediately above the marsh, there are four possible vegetation types: coastal grass meadow, *Elymus arenarius*, fresh *Carex* marsh, and *Honckenya peploides*, depending on landform configuration. Where the slope beyond tidal marsh is flat or gradually rising, it creates a tide-influenced meadow landform suitable for coastal grass meadow (Figure 2d). Mendenhall River, Lemon Creek, and Eagle River sand marsh have this configuration (Figure 3). Where the edge of tidal marsh reaches to a steep slope, the sequence is from a marsh vegetation type to a narrow *Elymus arenarius* upper marsh border (Figure 2c), as in Gastineau Channel marsh, Eagle River silt marsh, and along the sides of Lemon Creek and Eagle River sand marshes.

The landward slope of the tidal marsh at Mendenhall River and Lemon Creek-Switzer Creek is down instead of up (Figure 2b), so that fresh seepage water is ponded at the base of the valley sides, creating a habitat for fresh *Carex* marsh vegetation. The progression of vegetation types is from brackish-and-wet *Carex* tidal silt marsh to fresh-or-less-brackish-and-wet fresh *Carex* marsh and ends in ponds with mare's tail (*Hippuris tetraphylla*) as primary species (Figure 3). Tide-influenced coastal grass meadow can occur between the two types of *Carex* marsh.

The fourth sequence, marsh-to-*Honckenya peploides*, is less common than the marsh-to-*Elymus arenarius* sequence. It occurs in some parts of the Gastineau Channel marsh and Eagle River silt marsh, where the *H. peploides* vegetation type replaces the *Elymus arenarius* vegetation type as the upper marsh border (Figure 3).

Honckenya peploides is also an upper beach species on the outside of sand spits. It can occur there as the lowest elevation vegetation type just below *Elymus arenarius*. Whether the sequence is *H. peploides* - *E. arenarius* or *H. peploides* - *Elymus-Lathyrus* depends on the elevation of the lowest *E. arenarius* on the outside of the spit. *E. arenarius* can tolerate beating from waves, but beach pea (*Lathyrus maritimus*) cannot, so if *E. arenarius* is growing in the zone of storm waves, *Lathyrus* will be absent (Eagle River sand and silt marshes in Figure 3).

In the sampled coastal marshes around Juneau, the most common vegetation-type sequences from marsh to higher ground are: marsh - *Elymus arenarius* - (*Elymus-Lathyrus*) - coastal forb meadow; and marsh - coastal grass meadow - *Elymus arenarius* - (*Elymus-Lathyrus*) - coastal forb

meadow. *Elymus-Lathyrus* where present is often a narrow band between *Elymus arenarius* and coastal forb meadow on steep slopes above marshes. Since both *Elymus* and *Lathyrus* occur also as primary species in coastal forb meadow (Table 4), the progression *Elymus arenarius* - *Elymus-Lathyrus* - coastal forb meadow is apparently a consequence of differential reactions of species to the influence of tides and storms.

Habitat-Vegetation Complexes in Other Southeast Alaskan Coastal Marshes

The habitat-vegetation complex explains the differences in presence and arrangement of vegetation types in Juneau-area coastal marshes. If this concept is to be more generally useful, it must explain such differences elsewhere. Three other studies of southeast Alaskan coastal marsh vegetation reported in the literature (Stephens and Billings 1967, del Moral and Watson 1978, Watson 1981) contain enough habitat information to permit examination of the usefulness of the concept. Figure 4 shows the spatial relationships of the vegetation types in these studies. As in the Juneau area, no two marshes have the same vegetation-type composition or spatial arrangement of vegetation types. Because none of the studies was made on a completely physiographic basis, habitat-vegetation complexes cannot be defined, but they can be tentatively inferred from the published information combined with this author's field observations at two of the sites.

Stephens and Billings' (1967) description of the marsh at Kadashan Bay is most like the Juneau area marshes, with a sequence of *Carex* marsh - coastal grass meadow - upper marsh border. (The tufted hairgrass (*Deschampsia caespitosa*) community at Kadashan is inferred to be analogous to coastal grass meadow since *D. caespitosa* is a primary species of this vegetation type at Mendenhall River.)

Watson (1981) found five vegetation types in seven coastal marshes of the Sitka area (Figure 4). All marshes had different sequences of vegetation types along elevation gradients, but the types were consistently associated with particular substrates. Alkali grass (*Puccinellia nutkaensis*) was the assemblage at lowest elevations in all but one marsh. It occurred on silt and gravel. Because it has almost the same species composition as the *Puccinellia-Plantago* assemblage of the Juneau area and because *Carex lyngbyaei* is absent, it would appear

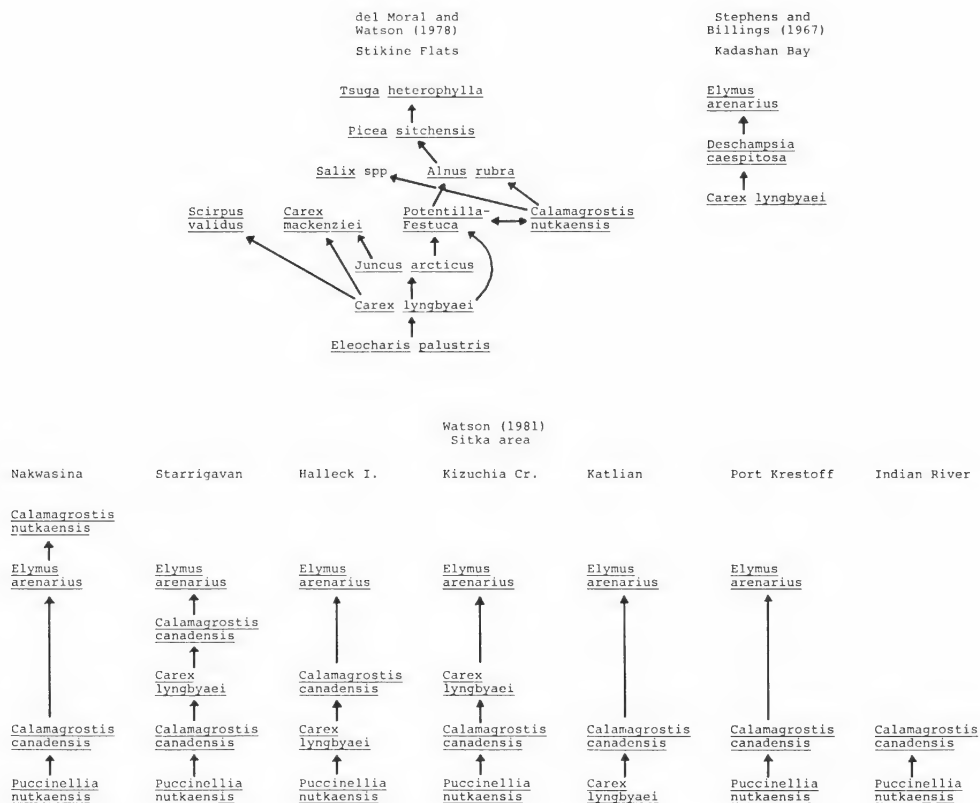


Figure 4. Variability in vegetation zonation of southeast Alaskan coastal marshes. Arrows point inland.

that Watson's *P. nutkaensis* assemblage is analogous to the Juneau area's complex 2, tidal grass-forb marshes on substrate coarser than silt. In all but one marsh, Watson's second assemblage inland is bluejoint (*Calamagrostis canadensis*). It grows on silt overlying gravel. This vegetation type is construed as analogous to tide-influenced meadow, because it occurs just below the *Elymus* upper marsh border in five of the seven marshes. Watson's *Carex lyngbyaei* assemblage on silt is presumed to be complex 1, tidal sedge and sedge-grass marshes on silt, because this complex is typical of brackish southeast Alaskan silt marshes (author's unpublished field observations). The *Calamagrostis nutkaensis* assemblage has a species composition resembling a mixture of the Juneau area's coastal grass meadow and coastal forb

meadow, but its position above the *Elymus* upper marsh border is supratidal. Thus, in location it is analogous to the Juneau area's coastal forb meadow.

The inconstant arrangement of the *Carex lyngbyaei* and *Calamagrostis canadensis* assemblages among Watson's marshes is puzzling. It would appear, however, that the explanation is physiographic. Watson found the *Calamagrostis canadensis* community most commonly growing on silt over gravel; *Carex lyngbyaei* occurred only on silt. The elevation range of maximum percent cover of *Carex lyngbyaei* was entirely within the elevation range of the *Calamagrostis canadensis* community. Therefore, the inconstancy of arrangement of these assemblages on Watson's elevation gradients cannot be the result of differences in tide-coverage

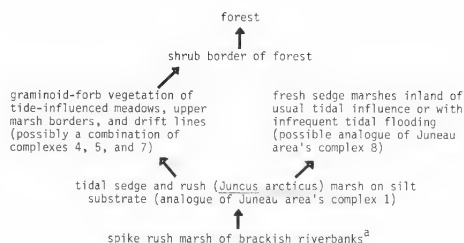
tolerance. It must be related to differences among marshes in distribution of silt and of silt overlying gravel. Because these differences result from physiographic processes, the relationship of vegetation types and substrate supports the concept of the habitat-vegetation complex as useful in understanding southeast Alaskan coastal marsh vegetation.

The Gastineau Channel vegetation diagram in Figure 3 indicates a way in which sequences such as Watson found at Halleck Island, Kizuchia Creek, and Starrigavan River might have come to be recorded. It is possible in the Gastineau Channel marsh to run a transect from the lowest elevation *Puccinellia-Plantago* through *Carex lyngbyaei*, another patch of *Puccinellia-Plantago*, into *Elymus arenarius* upper marsh border. The marsh floor along such a transect changes from sand, gravel, and cobbles, to silt to sand, gravel, and cobbles, to broken rock fill. Field observations in northern and central southeast Alaska indicate that this kind of substrate variability is usual in coastal marshes of this region. Therefore, a sequence of changes in substrate and/or elevation or landform and repetitions of these changes could be responsible for the repetitions of vegetation types along Watson's transects.

The sequence of vegetation types on the Stikine Flats (del Moral and Watson 1978, Sparks *et al.* 1977) is more complicated (Figure 4), because a larger area was sampled (4.5 km² vs. the 150 ha of the largest completely transected Juneau-area marsh) with four shrub and forest vegetation types in addition to marsh vegetation. Three communities of the Stikine Flats (*Calamagrostis nutkaten-sis*, *Potentilla-Festuca*, and *Carex mackenziei*) appear to be analogues of the Juneau area's coastal grass and forb meadow vegetation types in species composition and geographic/physiographic position (Table 1 and p. 4 in Sparks *et al.* 1977). Like these two vegetation types in the Juneau area, the three Stikine communities are described (p. 4) as "heterogeneous" and intergrading, with no strong dominants. Thus, in terms of habitat-vegetation complexes, the vegetation sequence at the Stikine Flats might be written as shown in Figure 5. A generalized arrangement of habitat-vegetation complexes for all coastal marshes studied so far in southeast Alaska is given in Figure 6.

Conclusion

Coastal marshes vegetation types and their habitat characteristics can be generalized into habitat-vegetation complexes, which allow us to make



^a observed also near Haines, Alaska (Stone, unpublished data, 1983, 1987)

Figure 5. Spatial arrangement of possible habitat-vegetation complexes on the Stikine Flats, southeast Alaska (inferred from Sparks *et al.* (1977)). Arrows point inland.

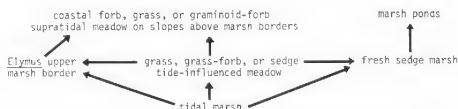


Figure 6. Generalized spatial arrangement of habitat-vegetation complexes in southeast Alaskan coastal marshes. Arrows point inland.

ecological comparisons of marshes with different sets of vegetation types. For southeast Alaska, the comparison is tentative outside the Juneau area because complete physiographic information is not available. Nevertheless, coastal marshes studied so far in southeast Alaska have a recognizable general arrangement of habitat-vegetation complexes. Even within the Juneau area this pattern varies because of the individualistic behavior of plant species and the differences in landform type and arrangement at different sites, and because of historical differences among marshes.

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Literature Cited

- Batten, A. R., S. Murphy, and D. R. Murray. 1976. Definition of Alaskan coastal wetlands by floristic criteria. Institute of Arctic Biology, University of Alaska, Fairbanks.
- Bertness, M. D., and A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecol. Monogr.* 57:129-147.
- del Moral, R., and A. F. Watson. 1978. Vegetation on the Stikine Flats, Southeast Alaska. *Northw. Sci.* 52:137-150.
- Egler, F. E. 1977. The Nature of Vegetation: Its Management and Mismanagement—An Introduction to Vegetation Science. Aton Forest, Norfolk, Conn.
- Federal Water Pollution Control Administration. 1966. Oceanographic and related water quality studies in Southeastern Alaska, August, 1965. US Dept. Inter., Fed. Water Pollut. Control Admin. Northwest Region, Portland, Oregon.
- Hack, J. T., and J. C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. U.S. Geol. Survey Professional Pap. 347.
- Hultén, E. 1968. Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford.
- Macdonald, K. B. 1977a. Plant and animal communities of Pacific North American salt marshes. In V. J. Chapman (ed.) *Wet Coastal Ecosystems*, Academic Press, New York. Pp. 167-191.
- . 1977b. Coastal salt marsh. In J. Major and M. G. Barbour (eds.) *Terrestrial Vegetation of California*, John Wiley and Sons, New York. Pp. 263-294.
- Macdonald, K. B. and M. G. Barbour. 1974. Beach and salt marsh vegetation of the North American Pacific Coast. In R. J. Reimold and W. H. Queen (eds.) *Ecology of Halophytes*, Academic Press, New York. Pp. 175-223.
- Miller, W. R., and F. E. Egler. 1950. Vegetation of the Wequetequock-Paucatuck tide-marshes, Connecticut. *Ecol. Monogr.* 20:143-172.
- Mueller-Dombois, D., and H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology*. John Wiley and Sons, New York.
- Raup, H. M. 1969. The relation of the vascular flora to some factors of site in the Mesters Vig district, Northeast Greenland. *Medd. Gron.* 176(5):1-216.
- . 1975. Species versatility in shore habitats. *J. Arnold. Arbor. Harv. Univ.* 55:126-165.
- Semeniuk, V., I. D. Cresswell, and P. A. S. Wurm. 1989. The Quindalup Dunes: the regional system, physical framework and vegetation habitats. *J. R. Soc. Western Australia* 71 (parts 2 and 3):23-47.
- Small, R. J. 1970. *The Study of Landforms: A Textbook of Geomorphology*. Cambridge University Press, London.
- Sparks, L. H., R. del Moral, A. F. Watson, and A. R. Kruckeberg. 1977. The distribution of vascular plant species on Sergief Island, southeast Alaska. *Syesis* 10:1-9.
- Stephens, F. R., and R. F. Billings. 1967. Plant communities of a tide-influenced meadow on Chichagof Island, Alaska. *Northw. Sci.* 41:178-183.
- Stone, C. S. 1984. Patterns in coastal marsh vegetation of the Juneau area, Alaska. Oregon State University, Corvallis. Ph.D. Dissertation.
- Watson, S. M. 1981. Wetlands habitat investigations in Sitka Sound, Alaska. Rep. to Alaska Dept. of Fish and Game, Anchorage, Alaska.
- Zimmermann, R. C., and B. G. Thom. 1982. Physiographic plant geography. *Progr. Phys. Geogr.* 6:45-59.

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Wintering Peregrine Falcon (*Falco peregrinus*) Habitat Utilization Near Sequim, Washington

Abstract

As DDT residues decrease in the environment, habitat loss becomes the number one threat to peregrine falcons (*Falco peregrinus*) in Washington. This state's population has grown, making it the second most densely populated Western state, and urban expansion threatens peregrine wintering areas in western Washington, including the area around Sequim. Three peregrine falcons were followed by radio-telemetry near Sequim, Washington to determine their habitat (resource) needs during winter, and to provide information to resource managers and planners in the Sequim area, and other similar areas. Two peregrines used two different habitats; an immature female utilized open water habitat significantly more than expected ($\alpha = 0.05$), while an immature male utilized grassy fields significantly more than expected. The home ranges for the male and female were 85.69 km² and 65.79 km² respectively. Ducks comprised 27% of the collected kills and 44% of other hunts (including missed attempts and uncollected kills). Passerines combined made up 42% of the collected kills and 26% of the other hunts. Conifer snags were the most common type of perch used.

Introduction

Peregrine falcons (*Falco peregrinus*) have been intensively studied since populations began declining in the late 1940's (Ratcliffe 1967, 1980) as a result of DDT residues accumulating in prey (Nelson 1969, Peakall *et al.* 1976). The presence of organo-pesticide contamination, however, is not the only threat to peregrine falcons. Land development is altering the habitats which support both the peregrine and its prey. Between 1960 and 1990 Washington State's human population grew by 70%, making it now the second most densely populated of the western states. Parts of Western Washington, where much of the recent growth has occurred, are important wintering areas for peregrines. In Clallam County, where Sequim is located, population growth has outstripped the rest of the state with an 85% increase in the last three decades. Population densities in Western Washington now equal those found in California, the most densely populated state in the west. Of the 3,760 km of marine shoreline in Washington 89% is privately owned, and while all estuarine environments have undergone modifications, 87% have seen moderate to severe changes. Urban areas are expanding onto wildlands more and more each year.

At least three western Washington areas are known to support winter resident peregrines: the Samish Flats (Anderson and DeBruyn 1979, Anderson *et al.* 1980), Grays Harbor (Dobler and Spencer 1987) and the Sequim area. All are at least somewhat associated with marine shorelines. In 1983, the area near Sequim was chosen for studies of wintering peregrine habitats because,

1) data compiled by the Washington Department of Wildlife and reports from raptor experts identified this area as a center of peregrine activity, and 2) residential development was creating potential conflicts. A better understanding of patterns of use might help preserve the peregrines here and in similar sites.

Study Area

Sequim lies near the northeastern corner of the Olympic Peninsula along the Strait of Juan de Fuca (Fig. 1) on a plain between the foothills of the Olympic Mountains and the strait. This fertile plain is a mixture of small farms and residential developments and is divided by the Dungeness River. Coniferous forests surround the farmlands on the undeveloped uplands and conifer stands grow interspersed throughout the area. Dungeness and Sequim bays form protected water bodies but offer only small areas of intertidal flats. Protection Island and Smith Island lie in the strait east and northeast of Sequim respectively. The area lies in the rain shadow of the Olympic Mountains and receives approximately 40 cm of rainfall.

Methods

Between 21 December 1983 and 21 March 1984, several field assistants and I captured three peregrines, using standard falconry techniques (Beebe and Webster 1985). An immature male (No. 5095) was captured on 4 January 1984, one immature female (No. 5049) was captured on 9 January 1984, and another immature female (No. 5022) on 10 February 1984. We fitted a six-gram

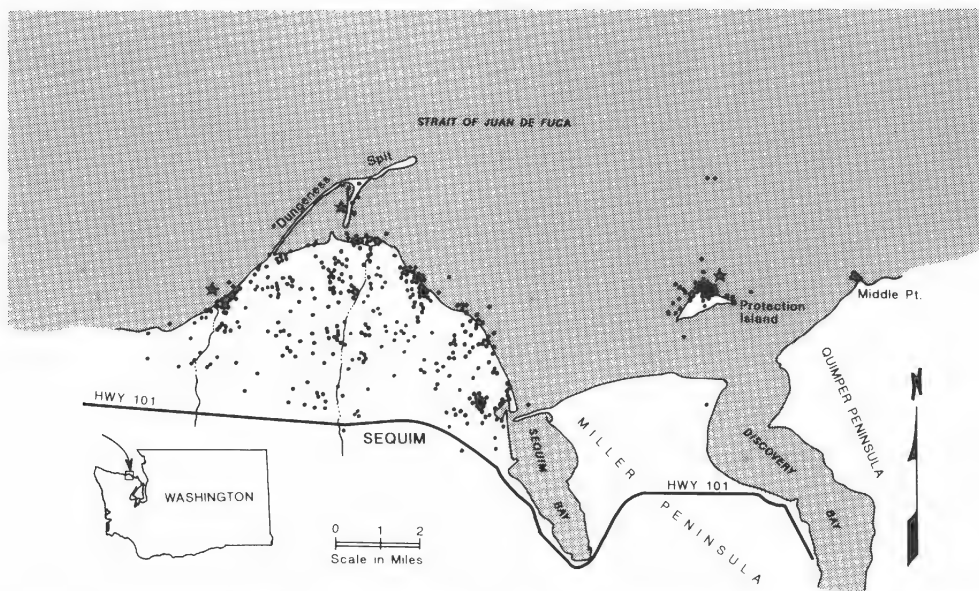


Figure 1. Vicinity map showing peregrine sighting locations. The points represent all observations (except Smith Island which is outside the area shown), and are not weighted by time. Stars are the locations of night roost sites.

transmitter to a central retrice of each bird, using methods similar to those described by Dunstan (1973). Using radio-telemetry, we located the birds and observed their behavior, recording all perch sites used and movements and noting the time at each change in activity. When a peregrine was seen with prey, we attempted to collect the prey remains after it had finished feeding and departed. In the course of searching for the radio-tagged birds we sometimes observed other peregrines, and recorded their activities as long as they could be observed.

I determined home ranges and core areas for the radio-tagged peregrines by using the harmonic mean measure of activity method (Dixon and Chapman 1980) and the computer program algorithm developed by Samuel *et al.* (1983). A core area is defined as the maximum area where the observed utilization distribution significantly differs from a uniform utilization distribution (Samuel *et al.* 1985). I weighted the calculations on the basis of time, using a maximum of one record for each half hour interval within an "observation." (An observation is an unbroken period of time. If a bird was lost for five minutes the next sighting became the start of a new observation period.) Each obser-

vation was given at least one record, regardless of the duration of the observation.

The Washington Department of Wildlife Remote Sensing Laboratory determined the habitat classifications utilized by the radio-tagged peregrines using LANDSAT remote sensing techniques. I then compared habitat utilization with availability based upon habitat composition within the home range boundaries and habitat composition of larger areas including the total home ranges. Simultaneous confidence intervals provided the means to compare utilization and availability (Marcum and Loftsgaarden 1980). Available habitat was defined by a boundary enclosing all the observed data points plus an arbitrary border about 2.5 km wide.

Results

There were 342 individual observations of peregrines during the study, with a total observation time of 225 hours. The radio-tagged immature male (bird 5095) accounted for 60 hours and one immature female (bird 5022) accounted for 79 hours. An injured immature female (bird 5049) accounted for 46 hours of observation. Non-radioed birds accounted for the remainder. A minimum of eight different peregrines used this study

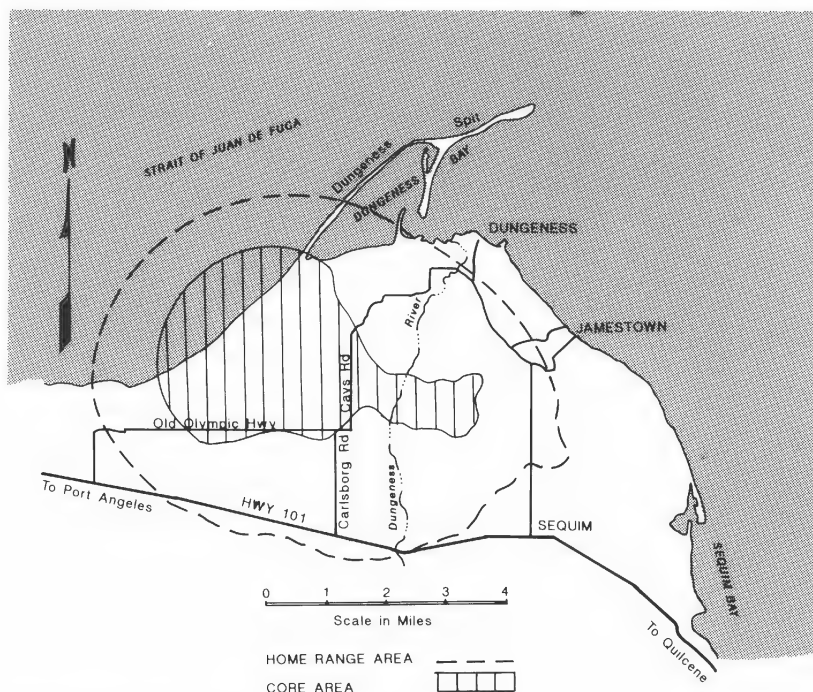


Figure 2. Home range of 5095, an immature male peregrine falcon.

area: three males, one adult and two immature; five females, one adult and four immatures. Six were seen repeatedly, one immature female was observed only two times and one immature male but once. In 21 cases peregrines were observed where individual identity could not be verified. Figure 1 shows locations of peregrine observations. Peregrine subspecies are not easily discernible in the field; however, all peregrines which could be carefully observed were judged to be *F. p. pealei*.

Peregrine No. 5049, had been shot and wounded by unknown persons with a .22 cal. rifle, at least two weeks prior to her capture 9 January, 1984. Her leg injury was apparent when she was first observed 28 December 1983. After capture she was taken to the Washington State Veterinary Clinic. Examination revealed a shattered leg that had mended on its own, although somewhat crooked. After a short observation period it was recommended that she be returned to the wild without treatment (Dr. Erik Stauber, pers. comm.). This bird was radio-tagged and released.

Bird 5095 had a calculated home range of 85.69 km² (Figure 2), and bird 5022 had a home

range of 65.79 km² (Figure 3). The core areas equaled 25.34 km² and 13.50 km² respectively. The injured female had a smaller home range than the other two birds, only 5.67 km² with a core area of 1.56 km².

Each of the home ranges contained a different habitat composition. Nine habitat classes were used for comparisons; water, coniferous forest, mixed forest, deciduous forest, shrub-woodland, grass-cropland, sparse grass, beach-bare ground, and other. Grass and cropland represented 62% of the male's home range, and open water comprised 23%. Seventy-two percent of the female's home range was open water, followed by grass and cropland with 15% of the total. Habitat utilization was not analyzed for No. 5049 since her injury might have influenced the size and shape of this home range.

Actual habitat use significantly departed from predicted habitat use ($\chi^2 = 1443.8$ for bird 5095, $\chi^2 = 556.4$ for bird 5022, $P < 0.005$, $df = 8$). Within the available habitats each bird showed different habitat choices. The male used the

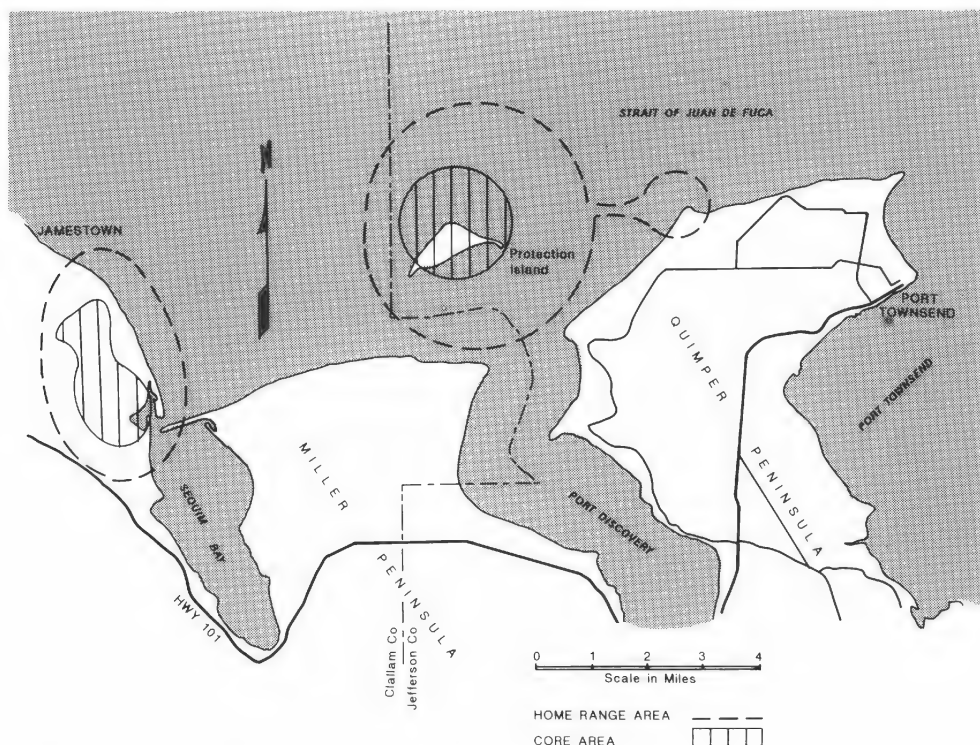


Figure 3. Home range of 5022, an immature female peregrine falcon.

grass-cropland habitat type significantly more than expected ($\alpha = .05$), and conifer forests and water significantly less than expected. The female used water significantly more than expected ($\alpha = .05$) over the total home range, and conifer woodlands, mixed forest and shrub-woodland, less than expected, with conifer woodlands comprising the largest area. Within the core area she used water significantly less than expected and used the categories grass-cropland, sparse grass and beach-bare ground more than expected on the basis of availability, although of these only grass-cropland contributed much to the total core area. Outside the core area these three categories had no higher use than the predicted value.

Feeding Habits

One peregrine, No. 4001, an adult male, used a site on Smith Island for perching and feeding. We collected all prey remains found at this perch site. All other prey remains came from separate loca-

tions where peregrines were actually observed feeding. Peregrines were observed to take or pursue members of 22 different species. Prey remains were collected from 33 kills and 86 other hunts were observed where prey identity was determined. Some of these other hunts ended in kills but prey remains were not collected and therefore are not represented in collected prey, but are included as other hunts. In addition three attempts to pirate from a gull were observed.

Twenty-seven percent of kills and 44 percent of the other hunts were waterfowl. While exact species was not always known, 65 percent of the identifiable waterfowl prey were from five species: bufflehead (*Bucephala albeola*), mallard (*Anas platyrhynchos*), wigeon (*Mareca americana*), green-winged teal (*Anas carolinensis*), and common goldeneye (*Bucephala clangula*). Thrushes, American robin (*Turdus migratorius*) and varied thrush (*Ixoreus naevius*), comprised 36 percent of the kills. Passerines combined made up 42 percent of the

kills and 26 percent of the other hunts. Mew gulls (*Larus canus*) were 3 percent of the kills but 17 percent of the other hunts. Attempts to capture cormorants were observed seven times (8% of the other hunts) and ancient murrelet (*Synthliboramphus antiquus*), and pigeon guillemot (*Cephus columba*) were each observed as prey two times, while rhinoceros auklet (*Cerorhinca monocerata*), black turnstone (*Arenaria melanocephala*), ring-necked pheasant (*Phasianus colchicus*) and merlin (*Falco columbarius*) were each observed as prey once.

Perch Selection and Roost Location

Peregrines in the Sequim area perched in snags 59 percent of the time (Total N = 636). Douglas fir (*Pseudotsuga douglasii*) and western red cedar (*Thuja plicata*) were the most commonly selected, being used 35 percent and 30 percent respectively. Conifer snags (all types combined) comprised 93 percent of the snags selected.

We located night roosts for the three radio-tagged peregrines (Figure 1). Bird 5095 regularly used a bluff near the mouth of McDonnell Creek, usually perching about 5 to 10 meters from the top in one of several depressions formed by erosion of the clay face. This is a north facing bluff along the Strait of Juan De Fuca. Bird 5022 used a bluff on the northeastern corner of Protection Island, also using the eroded clay face similar to bird 5095 above. The injured bird, 5049, roosted in the area of Graveyard Spit, although the exact location varied somewhat. Sometimes she roosted low, perhaps on the ground. At times she roosted on a navigation aide near the shore.

Discussion

The peregrines at Sequim made use of several different habitat types. Although only two home ranges were suitable for habitat preference analysis and represent only one season of use, the data do indicate that birds in the same general area use distinct habitats. The analysis can however overstate the importance of some habitat types and understate the importance of others. One bird (5022), used the shoreline and open water associated with it significantly more than expected over her entire home range, although within her home range core area, water was used less than expected. This is somewhat misleading. Certainly the shoreline was very important to her. However, because winter-

ing peregrines spend over 75 percent of the time perching (Anderson and DeBruyn 1979) and because her hunts usually began and ended with perching, the shoreline perching habit biased the core area analysis in favor of non-water habitats. However, if the direction of this bird's attention could have been considered in the analysis, the outcome would support the importance of the open water, for while her feet may have been on a firm tree branch, her gaze was nearly always out to sea. The harmonic mean analysis did not account for which way she was looking. In addition if our ability to track her over open water had been better its importance would have been even more pronounced. We often lost sight of her and were not able to gain adequate triangulation fixes, although at times the signal bearing changes suggested a meandering flight out over the water. On one occasion she was followed to Smith Island by boat, a distance of over 22 km, and was observed there on one other occasion. The adult male, while not radio-tagged and as a result seen far less frequently, showed a similar kind of behavior in the vicinity of Smith Island, indicating that use of this habitat is not limited to females.

Other peregrines spent much of their time further inland near the open fields and pastures. The immature male (bird 5095), roosted on the shoreline bluff, but almost always began his day by flying inland over fields, and usually remained there throughout the day. He would typically perch in tall snags near open fields, often moving across the landscape as successive hunts failed. His use of the open water was very infrequent. All the peregrines in the study area, both males and females, frequented marshes at least some of the time.

Sequim is adjacent to the Strait of Juan De Fuca, an area where diving ducks, grebes and other shallow water divers congregate in the winter (Wahl *et al.* 1981). It includes large open pastures where gulls and passerines feed. There are marshes and low areas where standing water attracts wintering ducks. These features all combine to form a diverse association of habitats which together support a variety of bird species, although the number of any one species is not particularly large. The 1983 Christmas Bird Count for the Sequim-Dungeness area reported 24,158 individuals of 127 species with only four species exceeding one thousand; wigeon (5,925), European starling (*Sturnus vulgaris*) (2,058), glaucous winged gull (*Larus glaucescens*) (1,925) and American

robin (1,024). Looking only at species of the size peregrines might consider for food, from medium sized gulls to finches, the Christmas Bird Count for the area recorded over 90 species and twenty thousand individuals.

No single group of prey represented a majority of the prey selected by peregrines at Sequim. In contrast observers in some other areas of Washington reported that peregrines primarily used one major group of prey species. In Grays Harbor, a major shorebird concentration area, dunlin (*Erolia alpina*) were selected 66% of the time (Dobler and Spencer 1987). On the Samish Flats, a major waterfowl wintering area, ducks were the main prey (Anderson and DeBruyn 1979, Anderson *et al.* 1980).

There has been an increasing transformation of the Sequim area from small farms with pastures and hay crops into residential developments. This change affects the suitability of habitats for peregrines wintering there. Although peregrines occasionally perch near houses, and hunt in backyards, human habitation creates some conflicts.

Increased dwelling density eliminates large open areas used by peregrines during hunts, thereby restricting pursuit and limiting capture success. In addition, increased housing density increases the likelihood of wire strikes, and shootings.

Some of the undeveloped lands are marshes. Development of marshes requires ditching and draining, which eliminates habitat for waterfowl, an important prey item. When human population density increases, snags, which are important perches for peregrine falcons, are removed, either for safety or for firewood. Habitat development along the shoreline may be especially destructive.

Literature Cited

- Anderson, C. M. and P. M. DeBruyn. 1979. Behavior and ecology of peregrine falcons wintering on the Skagit Flats, Washington: A report on the 1979 field season. Proj. No. E-1-WDG-PF-79-1. Washington State Game Department, Olympia, Wa. 53 pp.
- Anderson, C. M., P. M. DeBruyn, T. Ulm, and B. Gaussoin. 1980. Behavior and ecology of peregrine falcons wintering on the Skagit Flats, Washington: A report on the 1980 field season. Proj. No. E-1-WDG-PF-80-1. Washington State Game Department, Olympia, Wa. 54 pp.
- Beebe, F. L. and H. M. Webster, Eds. 1985. North American falconry and hunting hawks. 5th Ed. 400 pp. N. Am. Falconry and Hunting Hawks, Denver, CO.
- Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040-1044.
- Dobler, F. C., and R. D. Spencer. 1987. Wintering peregrine falcon, *Falco peregrinus*, habitat utilization in Grays Harbor, Washington. *Raptors in the Modern World*; Proceedings of the III World Conference on Birds of Prey and Owls. B. -U. Meyburg & R. D. Chancellor Eds. 71-78.
- Dunstan, T. C. 1973. A tail feather package for radio-tagging raptorial birds. *Inland Bird-Banding News* 45:3-6.
- Marcum, C. L. and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preferences. *J. Wildl. Manage.* 44:963-968.
- Nelson, M. W. 1969. The status of the peregrine falcon in the Northwest. Pp. 62-72. *Peregrine Falcon populations: Their biology and decline*. J. J. Hickey, Ed. Univ. Wisconsin Press, Madison.

The shoreline is often steeply banked with scenic possibilities for development. However the shorelines are critical to peregrines hunting the strait, particularly the snags and old trees growing along the edge. Some sites along the bank are also used as roosts. Increased human use of the shoreline areas, particularly any use of motorized vehicles on the narrow beach below the roost sites, will increase disturbance.

Peregrines tolerate human presence better than many other wildlife species, as exhibited by many nestings and winter sightings in metropolitan areas (Ratcliffe 1980). They will continue to use the Sequim area if key features of the shorelines, marshes, open fields and snags are maintained and some areas are protected from disturbance. Fortunately, the Protection Island National Wildlife Refuge protects one important shoreline site. Management of the refuge to maintain and enhance peregrine habitat and careful development of other lands will be required to conserve this species in this diverse habitat.

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- Peakall, D. B., L. M. Reynolds, and M. C. French. 1976. DDE in eggs of the peregrine falcon. *Bird Study* 23:183-86.
- Ratcliffe, D. A. 1967. Decreased eggshell weight in certain birds of prey. *Nature*(Lond.) 215:208-210.
- _____. 1980. *The peregrine falcon*. Buteo Books, Vermillion, South Dakota. 416 pp.
- Samuel, M. D., D. J. Pierce, E. O. Garton, L. J. Nelson, and K. R. Dixon. 1983. User's manual for program home range. For. Wildl. Rnge. Exp. Sta. Tech. Report 15. Moscow, ID pp 64.
- Samuel, M. D., D. J. Pierce, E. O. Garton. 1985. Identifying areas of concentrated use within the home range. *J. Animal Ecology* 54:711-719.
- Wahl, T. R., S. M. Speich, D. A. Manuwal, K. V. Kirsch, and C. Miller. 1981. Marine bird populations of the Strait of Juan de Fuca, Strait of Georgia, and adjacent waters in 1978 and 1979. Wildlife Science Group, College of Forest Resources, University of Washington, Seattle, WA. Prep. for MESA Puget Sound Project, EPA Interagency Agreement No. D6-E693-EN, Program Element No. EHE625-A. Office of Energy and Development, Office of Research and Development, U.S. Environ. Protect. Agency, Washington D.C. Doc. No. EPA-600/7-81-156.

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Stanley H. Anderson, USDI, Fish and Wildlife Service, Cooperative Fisheries and Wildlife Research Unit, Department of Zoology, University of Wyoming, Laramie, Wyoming 82071

Macrohabitat Associations of Merriam's Turkeys in the Black Hills, South Dakota

Abstract

Merriam's turkeys (*Meleagris gallopavo merriami*) were introduced into South Dakota in the late 1940's and have since expanded to occupy the entire Black Hills. Because little is known of their habitat requirements and the effects of forest management practices on this important game species, macrohabitat selections patterns of Merriam's turkeys in the Black Hills, SD were studied. Habitat units of 3-32 ha were delineated and described with methods used by the Forest Service for assessing impacts of management activities on wildlife. Winter habitats of turkeys were ponderosa pine (*Pinus ponderosa*) with greater than 70% overstory canopy cover. Summer habitats of turkeys were open ponderosa pine. Meadows were selected less than expected during all seasons. Resolution of conflicts over management of national forests depend largely on understanding of effects of management activities on wildlife species. Managing ponderosa pine at 14 to 18 m²/ha basal area in mature stands will reduce winter habitat for turkeys, but is consistent with summer habitat of adult turkeys without poults.

Introduction

Wild turkeys were not native to western South Dakota, but were transplanted in 3 separate releases of 8, 15, and 6 birds in 1948, 1950, and 1951, respectively (Peterson and Richardson 1973). Population estimates of turkeys in the Black Hills of South Dakota were 1,000 in 1952 and 5,000-7,000 in 1960; current estimates exceed 10,000.

Habitat use and management of the Merriam's (*Meleagris gallopavo merriami*) turkeys in nontraditional ranges have been studied in South Dakota (Peterson and Richardson 1975) and Montana (Rose 1956, Jonas 1966). Early studies of Merriam's turkey were limited by observation methods and contained biases in the assessment of the birds' habitat needs (e.g., Jonas 1966, Bryant and Nish 1975, Petersen and Richardson 1975, Shaw and Smith 1977). Telemetry has allowed collection of unbiased data on habitat use patterns, but few studies have been conducted in ponderosa pine (*Pinus ponderosa*) forest types (Mackey 1984, 1986, Schemnitz *et al.* 1985) and these have not addressed the detailed analyses of seasonal patterns of habitat selection. Habitats in prior studies were described vegetatively based on the dominant species of vegetation (Jonas 1966; Scott and Boeker 1975; Bryant and Nish 1975; Mackey 1982, 1986; Lutz and Crawford 1989) which precludes understanding the effects of forest management activities including logging or thinning

on Merriam's turkeys. Increased value of ponderosa pine timber resources, emphasis on old growth timber, and improved technology for harvesting timber have potential to impact Merriam's turkey habitat (Shaw 1986). The objectives of this study were to determine seasonal habitat use and selection patterns of Merriam's turkeys in a ponderosa pine ecosystem.

Study Area

This study was conducted in the central Black Hills of South Dakota, 16km west of Rapid City. The study area encompassed 4,380 ha. Most of the land area is under management by the Black Hills National Forest, Pactola Ranger District. Private holdings associated with ranch operations, private homes, and cabins are located in the study area.

Vegetation of the study area is primarily pure ponderosa pine forest (84%). Meadows and aspen (*Populus tremuloides*)/birch (*Betula papyrifera*) habitats occur in drainages, but some monotypic aspen habitats also occur on north exposures. Bur oak (*Quercus macrocarpa*) and white spruce (*Picea glauca*) comprise less than 1% of the study area. Climax vegetation or potential natural communities include: *Pinus ponderosa*/Symphoricarpos albus; *P. ponderosa*/Arctostaphylos uva-ursi; *P. ponderosa*/Juniperus communis; *Populus tremuloides*/Corylus cornuta; *Q. macrocarpa*/Ostrya virginiana; *Q. macrocarpa*/S. albus; and *Picea glauca*/Linnaea borealis Hoffman and Alexander (1987).

Geologic material is predominantly Precambrian and Cambrian granite, schists, and metasediments (Hoffman and Alexander 1987). Elevation ranges from approximately 1300 to 1800 m. Climate is continental with cold winters and warm summers (Orr 1959). January is typically the coldest month with mean temperature extremes of -11 to 2°C; July and August are the warmest with mean temperature extremes of 15 to 29°C. Average annual precipitation is 50 to 55 cm of which 70-80% falls between April and September (S. Dak. Climatological Summary, No. 20-39-6, U.S. Weather Bur.). Snowfall averages 84 cm, but may range from 25 to 200 cm. The combination of climate and soils is ideally suited for ponderosa pine, with dependable seed crops occurring regularly and excellent crops occurring at approximately 3-year intervals (Boldt and Van Duesen 1974).

Methods

This study was conducted over a 3-year period beginning March 1986 and ending January 1989. Some turkeys in the Black Hills used ranch feedlots and suburban housing developments for winter feeding; others remained in the forest throughout winter or until deep snow forced them to use ranches (Petersen and Richardson 1975). This research was conducted on birds in the latter category.

Turkeys were trapped during the study in late February or early March using rocket nets and drop nets over corn bait. This study focused on hens because of their importance to population growth or decline. Forty-four (36 females and 8 males) of 82 turkeys trapped were fitted with backpack radio transmitters weighing approximately 108 g.

Locations of birds began after a 1-week adjustment period to the radio transmitters (Nenno and Healy 1979). Each bird that remained in the study area was relocated 3 times each week. One location each week corresponded to each of the following time periods: sunrise to 1000 hr, 1001 to 1400 hr, and 1401 hr to sunset. Roosting habitats are included in Rumble (1992) and are not part of this paper. Birds that emigrated from the defined study area were relocated at least monthly to monitor their activities and determine if they moved back into the study area. Locations were determined by plotting 2+ bearings (frequently 5+) from known locations on USGS 1:24,000 con-

tour maps in the field using a handheld 2-element yagi antenna. Bearings were usually taken from positions that were within 300 m of the estimated location. Each location was assigned to a habitat unit (see below) based on maps and Universal Transverse Mercator coordinates and recorded to the nearest 100 m recorded in the field. To achieve independence of observations (Allredge and Ratti 1986), only 1 location was recorded for each bird on any given day and most were 2 days apart. Errors associated with assigning habitat units to locations were avoided by making location and habitat determinations in the field. Twenty-seven percent of all locations were either direct visual observations or telemetric locations of birds within about a 50-m radius circle within the determined boundaries of the habitat unit (Rumble 1990:16). Habitat assignments for bird's locations were facilitated by the topographic criteria used to determine habitat unit boundaries (see below).

Habitat Descriptions

Habitats in this study were numerically identified geographical units, used by the Forest Service to partition land areas for management. Boundaries were defined by watershed topography (ridges and drainages) or distinct changes in vegetation type. Private lands in the study area were assigned to habitats based on interpretation of 1:24,000 aerial photographs. Existing habitat boundaries were extended if the vegetation type was continuous, or new boundaries were assigned if changes in vegetation type were apparent.

Vegetative descriptions of habitats were made from estimates of dbh and basal area in each delineated habitat unit. Five plots, distributed evenly across each habitat unit, were marked on 1:24,000 contour maps in the laboratory. When habitat units were too small for effective placement of 5 plots, fewer plots were used. Each plot was then relocated in the field and sampled, with trees included in sampling determined using a 10-factor prism (Sharpe *et al.* 1976).

Descriptions of habitats were based on dominant species of vegetation and overstory canopy cover (Buttery and Gillam 1984). We did not stratify habitats on dbh classes because doing so did not improve understanding of habitat selection patterns of turkeys (Rumble and Anderson 1992). Overstory canopy cover (OCC) of ponderosa pine habitats was estimated based on the following

equation: $OCC(\%) = 0.51 * \text{BASAL AREA (FT}^2\text{/AC)} - 1.94$ (Bennett 1984). Aspen and birch habitats were combined because these species are managed as the same habitat by the Forest Service in the Black Hills. Our study included 513 habitat units from nine habitat categories which

included meadows, aspen/birch 0-40% OCC, aspen/birch 41-70% OCC, aspen/birch >71% OCC, ponderosa pine 0-40% OCC, ponderosa pine 41-70% OCC, ponderosa pine >71% OCC (Figure 1), spruce, and oak.

Figure 1. Major habitats represented in analyses of macrohabitat selection by Merriam's turkeys in the Black Hills, South Dakota.



A—Meadows



B—Aspen/Birch 0-40% overstory canopy cover



C—Aspen/Birch 41-70% overstory canopy cover



D—Aspen/Birch 71-100% overstory canopy cover

Figure 1. (Continued)



E—Ponderosa pine 0-40% overstory canopy cover



F—Ponderosa pine 41-70% overstory canopy cover



G—Ponderosa pine 71-100% overstory canopy cover

Analyses

Terminology used in this study follows Johnson (1980) and Thomas and Taylor (1990): *habitat use* implied utilization that was not compared to availability; *habitat selection* implied utilization that

was compared to availability; and *habitat preference* requires differential selection of resources given equal availability and was not part of this study.

Habitat use/selection data from turkeys were stratified into seasons; December-February (winter), March-May (spring), June-August (summer), and September-November (fall). To ensure that the assumption of independence of observations was maintained, analyses were done using only 1 observation if 2 or more radio-marked birds were located together.

Chi-square tests attempt to fit a specified model to a data set and significance indicates deviations from the expected fit under the model. The model in each test was no interaction among factors of the contingency table and hypotheses are stated in a positive sense (Steel and Torrie (1980:496-499). Chi-square test of independence was used to test the hypothesis that habitat use patterns of Merriam's turkeys were similar among seasons. This hypothesis was rejected ($P \leq 0.001$) and subsequent tests of habitat selection were made within seasons. Chi-square goodness-of-fit tests with correction for continuity (Cochran 1963) were used to test the hypotheses that within seasons, habitats selected by Merriam's turkeys were not different from random allocation of observations within habitats based on proportional area. Because oak, spruce, and aspen individually comprised a small portion of the study area, initial chi-square tests were made with oak and spruce pooled, and aspen habitats pooled to reduce as much as possible the number of cells with fewer than 5 expected observations. Deviations of habitat use versus expected use for individual habitats were made individually for all habitats including the three overstory categories of aspen habitats, oak habitats,

and spruce habitats, using Bonferroni Z-statistic confidence intervals around proportion of use (Neu *et al.* 1974, Byers *et al.* 1984) or by examination of chi-square residuals with G-standardization and Bonferroni correction to the Z-statistic if observed use was 0 (Mosteller and Parunak 1985). Significance of these confidence intervals hold regardless of the overall chi-square test (Neu *et al.* 1974).

Results

The hypothesis that habitat selection by Merriam's turkeys was similar to expected random allocation of observations within habitats was rejected ($P \leq 0.04$) for all seasons (Table 1). Aspen/birch habitats, 41-70% overstory canopy cover, were selected more than expected during spring and summer. Selection of aspen/birch habitats, 71-100% overstory canopy cover, was low over all seasons, but was less than expected only during spring. Open ponderosa pine habitats, 0-40% overstory canopy cover, were selected less than expected during the winter and spring. Ponderosa pine habitats, 41-70% overstory canopy cover, were selected equal to proportional availability during all seasons. Dense ponderosa pine habitats, 71-100% overstory canopy cover, were selected more than expected during fall and winter, and less than expected during summer. Meadows were selected less than expected during all seasons. Oak and spruce were not represented across all overstory canopy cover categories and comprised a small portion of the study area; therefore, few conclusions regarding selection of these habitats can be made except that use was infrequent during all seasons.

TABLE 1. Seasonal utilization by Merriam's turkeys of habitats described by dominant species and overstory canopy cover of vegetation in the Black Hills of South Dakota (modified from Rumble and Anderson 1992).¹

Habitat	Percent canopy cover	Proportional area	Winter (120) ²	Spring (427)	Summer (124)	Fall (193)
Aspen/birch	0- 40	0.015	0.017	0.023	0.024	0.005
Aspen/birch	41- 70	0.052	0--	0.080	0.090	0.036
Aspen/birch	71-100	0.018	0.008	0.002--	0.016	0.005
Ponderosa pine	0- 40	0.120	0.025--	0.084--	0.210	0.124
Ponderosa pine	41- 70	0.390	0.317	0.433	0.355	0.342
Ponderosa pine	71-100	0.341	0.558++	0.365	0.233--	0.440++
Meadows		0.102	0.058--	0.009--	0.040--	0.036--
Oak	0-100	0.004	0.017	0	0.008	0.005
Spruce	0-100	0.006	0	0.002--	0.024	0.005

¹Differences among habitats selected versus available, are indicated by -- if used less than expected and ++ if used more than expected.

²Sample sizes (telemetry fixes) are in parentheses.

Discussion

Over the course of a year, turkeys varied their habitat selection patterns to include nearly all ponderosa pine habitats. During fall and winter, turkeys apparently sought out ponderosa pine with greater than 71% overstory canopy cover; open ponderosa pine habitats were selected by turkeys infrequently during these seasons. Late October to early November was when turkeys began to spend increased amounts of time in the dense ponderosa pine habitats. Fall and winter habitat selection patterns were consistent with periods when diets of turkeys were composed primarily of ponderosa pine seeds (Rumble 1990). It is probable that thermal and hiding cover were better met in dense ponderosa pine habitats during late fall and winter.

Habitat selection of ponderosa pine stands reversed from summer to winter. Use of open habitats increased, but not significantly. However, selection of dense ponderosa pine habitats was less than expected during summer. Summer diets of adult turkeys, were comprised mostly of grass seeds and vegetation (Rumble 1990). Greater amounts of vegetation occur under ponderosa pine habitats with open canopies (Uresk and Severson 1989). Three-fourths of Merriam's turkeys observations in ponderosa pine communities in Montana were pole size stands with an open herbaceous understory Jonas (1966).

Meadows were rarely selected by turkeys. Openings in the forest are often utilized by turkeys in the southeastern United States (Speake *et al.* 1975), in the southwest (Scott and Boeker 1977), and in Montana (Jonas 1966). Oak and spruce habitats comprised less than 1% of the study area, and few meaningful statistical patterns were evident. However, during years with good oak mast production, turkeys used oak habitats for 2-4 weeks in September and October. This suggests that the limited importance of oak habitats in our study was due to the narrow distribution of oak on the study area and irregularity of mast crops.

Aspen/birch habitats selected by turkeys in our study were primarily in drainages rather than monotypic aspen habitats that occurred on some north slopes. Winter foods of turkeys were not as available in aspen/birch habitats (Rumble 1990). However, aspen/birch habitats were used more during spring, summer, and fall. These habitats contained an abundance of grasses, forbs, and shrubs, which dominated late spring, summer, and

early fall diets of turkeys (Rumble 1990). Turkeys in Utah used aspen glades (openings) as opposed to monotypic aspen habitats during summer (Bryant and Nish 1975).

Distribution of water affects habitat dispersion patterns of Merriam's turkeys in the southwest (Shaw and Smith 1977, Schemnitz *et al.* 1985). Spring weather conditions during this study were dry and some aspen/birch drainages had running water in them. Birds increased use of aspen/birch habitats with less than 70% overstory canopy cover during spring, but not statistically greater than expected from random. Free-standing water may not be required by turkeys in all habitats (Exum *et al.* 1987). Outside of the spring period, we observed turkeys at free-standing water on fewer than 10 occasions. The primary factor affecting the association of turkeys to water reported by Schemnitz *et al.* (1985) was feeding on watercress (*Nasturium officinale*) during winter.

Management Implications

Conflicts regarding management of the Black Hills National Forest can only be resolved if the effects of management actions on the wildlife species are understood. The Land and Resource Management Plan for the Black Hills National Forest proposes managing ponderosa pine habitats at 14 or 18 m²/ha projected tree basal area when the average dbh of the stand is 25 cm. Basal area would be higher for larger diameter trees and lower for smaller diameter trees. During winter, Merriam's turkeys selected ponderosa pine habitats with greater than 70% overstory canopy cover and greater 32 m²/ha basal area. Thirty-four percent of our study area was winter habitat for turkeys. Managing ponderosa pine stands to 14 or 18 m²/ha basal area in mature stands will reduce availability of winter habitat for turkeys in the Black Hills. However, managing stands to 14 to 18 m²/ha basal area would be consistent with summer habitats of adult turkeys without poults. On an annual basis, turkeys selected the full range of ponderosa pine habitats that occur in the Black Hills. If turkeys are a management priority, winter habitat should be abundant and well distributed (Hoffman *et al.* 1993) at lower elevations of the Black Hills. Management directed toward maintaining habitats in all of overstory canopy cover categories within vegetation types would ensure that habitat needs for turkeys would be met as well as many other wildlife species (Hoover and Wills 1984).

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Literature Cited

- Allredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* 50:157-165.
- Bennett, D. L. 1984. Grazing potential of major soils within the Black Hills of South Dakota. S. Dak. State Univ., Brookings. M.S. Thesis.
- Bryant, F. C., and D. Nish. 1975. Habitat use by Merriam's turkey in southwestern Utah. *Proc. Natl. Wild Turkey Symp.* 3:6-13.
- Buttery, R. F., and B. C. Gillam. 1983. Forest ecosystems. In R. L. Hoover and D. L. Wills (eds.), *Managing forested lands for wildlife*. Col. Div. Wildl. in cooperation with USDA For. Serv., Rocky Mtn. Region., Denver. Pp. 34-71.
- Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48:1050-1053.
- Cochran, W. G. 1963. *Sampling Techniques*. John Wiley and Sons, New York. 413 p.
- Exum, J. H., J. A. McGlinchy, D. W. Speake, J. L. Buckner, and F. M. Stanley. 1987. Ecology of the eastern wild turkey in an intensively managed pine forest in southern Alabama. *Tall Timber Res. Stn. Bull. No. 23*. Tallahassee, FL. 70 p.
- Hoffman, G. R., and R. R. Alexander. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat type classification. USDA For. Serv. Res. Pap. RM-276. Rocky Mtn. For. Range Exp. Stn., Fort Collins, Colo. 48 p.
- Hoffman, R. W., H. G. Shaw, M. A. Rumble, B. F. Wakeling, C. M. Molohan, S. D. Schemnitz, R. Engel-Wilson, and D. A. Hengel. 1993. Management guidelines for Merriam's wild turkeys. Div. Rep. No. 18. Colo. Div. Wildl. in coop. with USDA For. Serv. Rocky Mtn. For. Range Exp. Stn. Fort Collins, Colo. 24p.
- Hoover, R. L., and D. L. Wills, ed. 1984. *Managing forested lands for wildlife*. Colo. Div. Wildl. in coop. USDA For. Serv., Rocky Mtn. Reg., Denver, Colo. 459p.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Jonas, R. 1966. Merriam's turkeys in southeastern Montana. *Tech. Bull. No. 3*. Mont. Game and Fish Dept., Helena. 36 p.
- Lutz, R. S., and J. A. Crawford. 1989. Habitat use and selection of home ranges of Merriam's turkey in Oregon. *Great Basin Nat.* 49:252-258.
- Mackey, D. L. 1982. Ecology of Merriam's turkeys in south central Washington with special reference to habitat utilization. Wash. State Univ., Pullman. M.S. Thesis.
- _____. 1984. Roosting habitat of Merriam's turkeys in south-central Washington. *J. Wildl. Manage.* 48:1372-1382.
- _____. 1986. Brood habitat of Merriam's turkeys in south-central Washington. *Northwest Sci.* 60:108-112.
- Mosteller, F., and A. Parunak. 1985. Identifying extreme cells in a sizeable contingency table: probabilistic and exploratory approaches. In D. C. Hoaglin, F. Mosteller, and J. W. Tukey (eds.), *Exploring data tables, trends, and shapes*. John Wiley and Sons, New York. Pp. 189-224.
- Nenno, E. S., and W. M. Healy. 1979. Effects of radio packages on behavior of wild turkey hens. *J. Wildl. Manage.* 43:460-465.
- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541-545.
- Orr, H. K. 1959. Precipitation and stream flow in the Black Hills. USDA For. Serv. Stn. Pap. RM-44. Rocky Mtn. For. Range Exp. Stn., Fort Collins, CO. 25 p.
- Petersen, L. E., and A. H. Richardson. 1973. Merriam's wild turkey in the Black Hills of South Dakota. In G. C. Sanderson and H. C. Schultz (eds.), *Wild turkey management: current problems and programs*. Univ. Missouri Press, Columbia. Pp. 3-9.
- _____, and _____. 1975. The wild turkey in the Black Hills. S. Dak. Dept. Game, Fish and Parks. Bull. No. 6., Pierre. 51 p.
- Rose, B. J. 1956. An evaluation of two introductions of Merriam's wild turkey to Montana. *Mont. State Coll., Bozeman*. M.S. Thesis.
- Rumble, M. A. 1990. Ecology of Merriam's turkeys (*Meleagris gallopavo merriami*) in the Black Hills, South Dakota. Univ. Wyo., Laramie. Ph.D. Dissertation.
- _____. 1992. Roosting habitat of Merriam's turkeys in the Black Hills, South Dakota. *J. Wildl. Manage.* 56:750-759.
- Rumble, M. A., and S. H. Anderson. 1992. Stratification of habitats for identifying habitat selection by Merriam's turkeys. *Great Basin Nat.* 52:139-144.
- Schemnitz, S. D., D. L. Goerndt, and K. H. Jones. 1985. Habitat needs and management of Merriam's turkey in south-central New Mexico. *Proc. Natl. Wild Turkey Symp.* 5:199-232.
- Scott, V. E., and E. L. Boeker. 1975. Ecology of Merriam's wild turkey on the Fort Apache Indian Reservation. *Proc. Natl. Wild Turkey Symp.* 3:141-158.
- _____. 1977. Responses of Merriam's turkey to pinyon-juniper control. *J. Range Manage.* 30: 220-223.
- Sharpe, G. W., C. W. Hendee, and S. W. Allen. 1976. *Introduction to forestry*. McGraw-Hill, New York. 544 p.

- Shaw, H. G., and R. H. Smith. 1977. Habitat use patterns of Merriam's turkey in Arizona. Fed. Aid Wildl. Restor. Proj. W-78-R. Ariz. Dept. Game and Fish, Tucson. 33 p.
- . 1986. Impacts of timber harvest on Merriam's turkey populations. Problem Analysis Report. Ariz. Dept. Game and Fish, Tucson. 44 p.
- Speake, D. W., T. E. Lynch, G. A. Wright, and W. J. Hamrick. 1975. Habitat use and seasonal movements of wild turkeys in the southeast. Proc. Natl. Wild Turkey Symp. 3:122-130.
- Steel, R. D. G., and J. H. Torrie. 1980. Principals and procedures of statistics: a biometrical approach. McGraw-Hill Book Co. 633 p.
- Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manage. 54:322-330.
- Uresk, D. W., and K. E. Severson. 1989. Understory-overstory relationships in ponderosa pine forests. J. Range Manage. 42:203-208.

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D. Ganskopp, USDA-ARS N. Great Basin Exp. Range, HC 71 4.51 Hwy. 205, Burns, Oregon 97720

B. Myers, Soil Conservation Service, P.O. Box 848, Hines, Oregon 97738

and

S. Lambert, Soil Conservation Service, US Court House Rm 360, West 920 Riverside, Spokane, Washington 99201.

Black-tailed Jackrabbit Preferences for Eight Forages Used for Reclamation of Great Basin Rangelands¹

Abstract

During peak periods of their population cycles black-tailed jackrabbits (*Lepus californicus*) may compete with other herbivores for forage and negatively impact the health and production of the forage resource. This study was conducted on the Northern Great Basin Experimental Range near Burns, Oregon. Our objective was to establish the growing season relative preferences of jackrabbits for eight selections of grasses available for reclamation of Great Basin rangelands. Response variables included percent of plants defoliated and degree of utilization from plots supporting equal numbers of all selections. The percent of plants grazed and utilization levels of two crested wheatgrass cultivars were nearly twice those of the other grasses. Two cultivars of basin wildrye and one selection of Russian wildrye were avoided by jackrabbits, while one cultivar of bluebunch wheatgrass and two selections of thick-spiked wheatgrass were passively foraged upon. Seedlings of unpalatable cultivars are suggested to: (1) discourage jackrabbit presence in right-of-ways where they pose a danger, (2) to reduce competition between jackrabbits and livestock for forage, or (3) reduce potential damage to ground cover or forage resources in critical areas during jackrabbit population peaks. Conversely, seedlings of palatable cultivars might be used to lure jackrabbits away from less palatable, but more valuable crops or forages.

Introduction

Black-tailed jackrabbits (*Lepus californicus*) frequent North American range and croplands from Washington, east to the Dakotas in the United States, and extend south into Mexico (Hall 1981). Jackrabbit populations are cyclic, with 7 to 10 years typically separating peak numbers (Gross *et al.* 1974). When high populations occur, jackrabbits can compete with wild and domestic herbivores for forage (Currie and Goodwin 1966, Johnson 1979). Many feel that high populations of these animals affect stature and composition of rangeland vegetation through selective grazing (Stewart and Hull 1949, Sparks 1968, Uresk 1978, Roundy *et al.* 1985, Crawley 1990). Others suggest, however, that because populations are cyclic, and the hares exert feeding pressure on nearly all important components of plant communities, they have little influence on vegetation composition of good condition rangelands (Anderson and Shumar 1986).

Agricultural crops and reclaimed rangelands, particularly crested wheatgrass (*Agropyron desertorum* (Fischer ex Link) Schultes) seedlings, are often preferred by black-tailed jackrabbits (Fagerstone *et al.* 1980, Roundy *et al.* 1985). Jackrabbits select grasses in early spring and

summer, forbs in late summer and fall, and shrubs during winter months (Currie and Goodwin 1966, Sparks 1968). The spring and early summer period coincides with the late-boot and early anthesis stages of phenology of our caespitose grasses, a period when severe defoliation may significantly affect vigor or health of these plants (McIlvanie 1942, Cook *et al.* 1958, Ganskopp 1988). Reclamation or revegetation specialists may avoid potential stand failures and competition for forage if information on relative preferences of black-tailed jackrabbits for common cultivars was available.

We evaluated the relative preferences of black-tailed jackrabbits for eight selections of grasses adapted to and available for reseeding areas in the arid Great Basin. Selections (and recommended precipitation ranges for planting) were: 2 cultivars of basin wildrye (*Leymus cinereus* (Scribner & Merrill A. Löve)), Magnar (20-63 cm) and Trailhead (20-41 cm); 1 cultivar of bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Goldar (20-46 cm); 2 cultivars of thick-spiked wheatgrass (*Elymus lanceolatus* ((Scribner & J.G. Smith)Gould), selection #9021076 (15-41 cm) and Secar (20-46 cm); the Bozoisky (31-36 cm) cultivar of Russian wild-rye (*Psathyrostachys junceus* (Fischer)Nevsk); Nordan crested wheatgrass (*Agropyron desertorum* (Fischer ex Link) Schultes) (20-30 cm); and a crested wheatgrass cross called

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Hycrest II (20-20 cm), a product of *Agropyron desertorum* and *Agropyron cristatum* (L.) Gaertner). Our objective was to identify selections which might be attractive to or avoided by black-tailed jackrabbits. This was accomplished by monitoring frequency and intensity of utilization of plants by native black-tailed jackrabbits having access to plots where all selections were equally available.

Materials and Methods

The study was conducted on the Northern Great Basin Experimental Range (119°43'W, 43°29'N) 70 km west-southwest of Burns, OR. Mean annual precipitation is 28 cm with peak monthly accumulations in November, December, January, and May (ranging from 2.8 to 3.6 cm); and a mean minimum accumulation (0.8 cm) in July. Mean annual temperature is 7°C with extremes of -29 and 42°C. Mean crop-year precipitation (Sept.-June) is 23 cm. Soil where plots were established was a Holte (coarse-loamy, mixed, frigid Aridic Duric Haploxerolls) Milcan (coarse-loamy, mixed, frigid Orthodic Durixerolls) complex (Lentz and Simonson 1986).

With the exception of Hycrest II, from USDA-ARS Logan, UT, seed was acquired from the SCS Pullman Plant Materials Center, Washington. Seedlings were established in tubes in a green house during the winter and transplanted to plots in early April 1990. Crop-year precipitation for 1990 was 74% of average, but because plants were growing essentially free from competition, they tillered prolifically. Planting design was a randomized complete block with eight treatments (cultivars) and nine replications. A replicate contained 98 plants of each selection (total/replicate = 784 plants) randomly planted within a 28 X 28 matrix. Matrix rows and columns were 76 cm apart with each of the nine replicates being 20.6 m to a side. Plots were kept weed-free by mechanical means. Vegetation adjacent to the plots was native sagebrush (*Artemisia* spp.)/bunchgrass to the west and crested wheatgrass to the north, east and south. Herbage production, sampled for an unrelated project in one of our adjacent crested wheatgrass pastures, was 294 kg/ha (± 6.0 , 95% CI). Although we did not sample production in our plots, the level of herbage available appeared to equal or slightly exceed that of the neighboring crested wheatgrass. Production in the native sagebrush/bunchgrass vegetation appeared to be lower than the neighboring crested wheatgrass pastures. Small rodents, primarily

Townsend ground squirrels (*Spermophilus townsendi*), were eliminated both within and adjacent to the plots with zinc phosphide. Trails, frequent sightings, and jackrabbit scat on nearly every square meter of our plots gave us confidence that black-tailed jackrabbits were the main herbivores.

Jackrabbits from surrounding terrain had free access to the plots from early June until 10 July 1990. Most foraging was nocturnal, and we did not census the animals. One would, however, typically encounter a jackrabbit for every 50 to 75 m of day-time travel in the adjacent sagebrush/bunchgrass vegetation. Night road surveys of jackrabbit numbers in Harney County have been compiled by Oregon Department of Fish and Wildlife personnel for the last 12 years and indexed as numbers/100 km traveled. Variation is extreme, and numbers range from 0 in 1985 to a high of 183/100 km in 1981. The mean and standard deviation for this same period are 46 and 58.7/100 km, respectively. The index for 1990 was 40/100 km (personal communication, George Keister, Or. Dept. Fish & Wildl.).

During the period the jackrabbits had access to plots, plants were in the vegetative and early-boot stages of phenology. The latter stage is the time when severe defoliation most negatively affects subsequent vigor and production of cool-season grasses (McIlvanie 1942, Cook *et al.* 1958, Ganskopp 1988). Diameters of individual plants ranged between 3 and 12 cm. After hares were excluded from plots by fencing, each plant was scored for presence or absence of any sign of defoliation, indexed as either a 0 or a 1, and degree of utilization as indexed by scores ranging from zero to three. Scores, based on appearance of plants, indicated: 0) no utilization, 1) 1-20% herbage weight removed, 2) 20 to 40% weight removed, and 3) >40% weight removed. Scores ($n=98$) for both response variables were summed by cultivar ($n=8$) within each replication ($n=9$) with the totals functioning as single observations ($n=72$) in randomized-complete-block analyses of variance. Data were converted to percentages after analyses.

Mean separations and preference ratings were accomplished with Least Significant Difference (LSD) procedures ($P=0.05$). Selections scoring > than 1 LSD above the mean were viewed as "preferred," those <1 LSD below the mean were recognized as "avoided," and those within ± 1 LSD of the mean were considered to be "passively"

foraged upon by jackrabbits. Degree of association between relative rankings established for the selections by the two response variables was quantified with Spearman's rank correlation coefficient (Gibbons 1971).

Results and Discussion

Approximately 34% of all plants received some degree of defoliation with the range extending from 4% for "Trailhead" basin wild-rye to 69% for "Hycrest II" crested wheatgrass. Mean percentages of plants defoliated ($F=61.4$ with 7 and 56 df) and levels of utilization ($F=57.9$ with 7 and 56 df) by black-tailed jackrabbits differed significantly among selections with nearly identical interpretations derived from both response variables (Figures 1 and 2). The crested wheatgrass cultivars (Nordan and Hycrest II) were clearly preferred forages. Percent of plants defoliated and levels of utilization for both cultivars were nearly two times greater than scores of the other selections, and approximately 6% of

these plants were actually killed by overgrazing. The bluebunch wheatgrass cultivar (Goldar) and the two thick-spiked wheatgrasses were foraged upon at roughly mean levels and were assigned a passive rating. The Bozoisky Russian wild-rye and two basin wild-rye cultivars, Trailhead and Magnar, were lightly foraged upon and ranked as avoided. Relative rankings among selections were nearly identical between the two response variables (Spearman's coefficient of rank correlation $r_s=0.98$) with the only discrepancy being a non-significant ($P>0.05$) exchange of "Secar" and thick-spiked wheatgrasses as ranked by the two indices (Figures 1 and 2).

Our results suggest these cultivars could be used as management tools to either discourage or encourage black-tailed jackrabbit use of an area. For example, plantings of the wildrye cultivars might avoid attraction to road or aircraft runway right of ways. In a similar vein, the basin and Russian wild-rye cultivars might function as protective

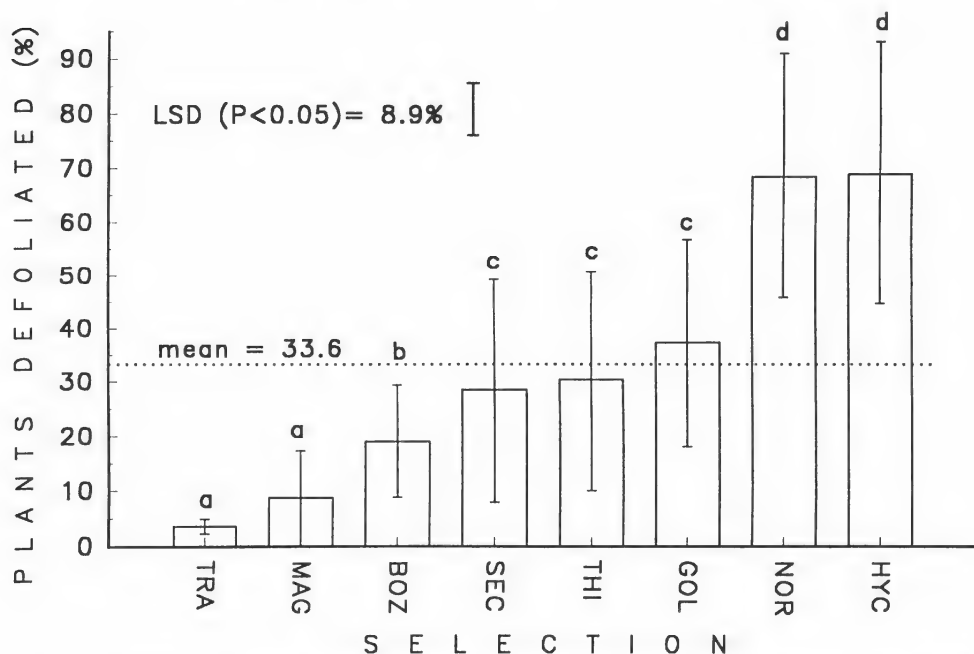


Figure 1. Percentages of plants defoliated by black-tailed jackrabbits among eight selections of grasses at the Northern Great Basin Experimental Range. Selections are, respectively: Trailhead basin wildrye (TRA), Magnar basin wildrye (MAG), Bozoisky Russian wildrye (BOZ), Secar bluebunch wheatgrass (SEC), thickspike wheatgrass (THI), Goldar bluebunch wheatgrass (GOL), Nordan crested wheatgrass (NOR), and Hycrest II crested wheatgrass (HYC). Error bars denote ± 1 standard deviation of the mean for each cultivar. Columns sharing a common letter are not significantly different ($P>0.05$).

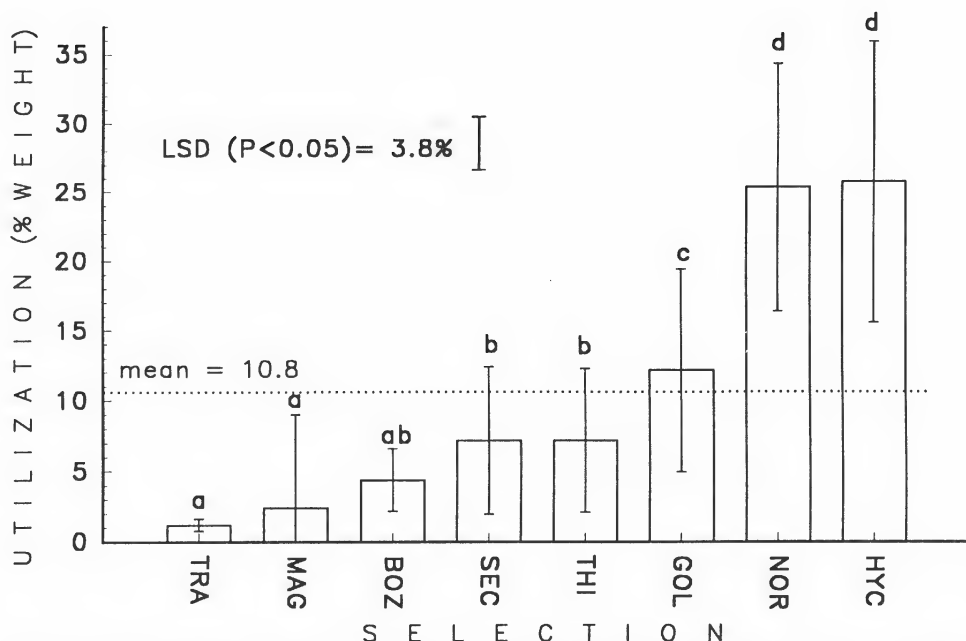


Figure 2. Percent utilization reflecting amount of material removed from eight selections of grasses by black-tailed jackrabbits at the Northern Great Basin Experimental Range. Selection abbreviations are referenced in Figure 1 heading. Error bars denote ± 1 standard deviation of the mean for each cultivar. Columns sharing a common letter are not significantly different ($P > 0.05$).

buffers around more valuable crops as suggested by Fagerstone *et al.* (1980) or as alternative livestock forages less likely to be consumed or damaged by black-tailed jackrabbits. Conversely, plantings of crested wheatgrass cultivars might lure jackrabbits away from more valuable, but less palatable, crops or critical areas. Efficacy of buffer strips for crop protection has not been tested, however, and additional research is needed to address applicability of this hypothesis.

In the sagebrush-steppe, black-tailed jackrabbits typically inhabit shrub dominated areas during daylight and make feeding forays into areas offering higher quality forage but less overhead cover at night (Johnson and Anderson 1984). Research by Longland (1991) detected significantly less use of palatable feed by jackrabbits when distance from cover was only 5 to 10 m. Under more applied conditions, in large seedings, and with high populations, black-tailed jackrabbits typically forage within a 300-m band adjacent to protective cover (Westoby and Wagner 1973, Roundy *et al.*

1985, McAdoo *et al.* 1987). We saw no significant evidence of a utilization gradient in our plots which ranged from 5 to 65 m from protective shrubs. Percent of plant weight utilized averaged 9% for the 3 replications closest to cover and 12% in the 3 most distant blocks. The fact that crested wheatgrass bounded our plots on 3 sides raises the possibility that jackrabbits might have been preconditioned to select these cultivars. The duration (about 40 days) of this trial, however, was sufficient to allow the hares to develop selective priorities. Indeed, in more controlled preference experiments, animals are frequently given much less acclimation time and forced to deplete their forage resources to a greater degree (Currie and Goodwin 1966, Murray 1984). Additionally, our observations indicated the hares occupied the sagebrush/bunchgrass vegetation during daylight hours where they had access to a diversity of native grasses as well.

Our findings, and those of others (Johnson and Anderson 1984, Crawley 1990) clearly demonstrate

selective grazing by black-tailed jackrabbits. Having identified favored and avoided cultivars, we suggest planting avoided selections in areas prone to frequent out-breaks of black-tailed jackrabbits. Possible benefits include: (1) minimizing potential damage to growing forage or arid land ground

cover during its most susceptible stage of phenology, (2) reducing competition with livestock or other wildlife for forage, and (3) perhaps discouraging immigration and/or encouraging emigration of these hares to other areas.

Literature Cited

- Anderson, J. E., and M. L. Shumar. 1986. Impacts of black-tailed jackrabbits at peak population densities on sagebrush-steppe vegetation. *J. Range Manage.* 39:152-156.
- Cook, C., L. Stoddart, and F. Kinsinger. 1958. Responses of crested wheatgrass to various clipping treatments. *Ecol. Monogr.* 28:237-272.
- Crawley, M. J. 1990. Rabbit grazing, plant competition and seedling recruitment in arid grassland. *J. App. Ecol.* 27:803-820.
- Currie, P. O., and D. L. Goodwin. 1966. Consumption of forage by black-tailed jackrabbits on salt-desert ranges of Utah. *J. Wildl. Manage.* 30:304-311.
- Fagerstone, K. A., G. K. Lavoie, and R. E. Griffith, Jr. 1980. Black-tailed jackrabbit diet and density on rangeland and near agricultural crops. *J. Range Manage.* 33:239-233.
- Ganskopp, D. 1988. Defoliation of thurber needlegrass:herbage and root responses. *J. Range Manage.* 41:475-478.
- Gibbons, J. D. 1971. Nonparametric statistical inference. McGraw Hill, New York.
- Gross, J. E., L. C. Stoddart, and F. H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. *Wildl. Monogr.* 40:63.
- Hall, E. R. 1981. The mammals of North America. 2nd. ed., Wiley, New York.
- Johnson, M. K. 1979. Foods of primary consumers on cold desert shrub-steppe of southcentral Idaho. *J. Range Manage.* 32:365-368.
- Johnson R. D., and J. E. Anderson. 1984. Diets of black-tailed jack rabbits in relation to population density and vegetation. *J. Range Manage.* 37:79-83.
- Lentz, R. D., and G. H. Simonson. 1986. A detailed soils inventory and associated vegetation of Squaw Butte Range Experiment Station. Agr. Exp. Sta. Oregon State Univ., Corvallis. Special Rep. 760.
- Longland, W. S. 1991. Risk of predation and food consumption by black-tailed jackrabbits. *J. Range Manage.* 44:447-450.
- McAdoo, J. K., W. S. Longland, G. J. Cluff, and D. A. Klebenow. 1987. Use of new rangeland seedlings by black-tailed jackrabbits. *J. Range Manage.* 40:520-524.
- Mellvanie, S. 1942. Carbohydrate and nitrogen trends in blue-bunch wheatgrass, *Agropyron spicatum*, with special reference to grazing influences. *Plant Physiol.* 17:540-557.
- Murray, R. B. 1984. Yields, nutrient quality, and palatability to sheep of fourteen grass accessions for potential use on sagebrush-grass range in southeastern Idaho. *J. Range Manage.* 37:343-348.
- Roundy, B. A., G. J. Cluff, J. K. McAdoo, and R.A. Evans. 1985. Effects of jackrabbit grazing, clipping, and drought on crested wheatgrass seedlings. *J. Range Manage.* 38:551-555.
- Sparks, D. 1968. Diet of black-tailed jackrabbits on sandhill rangeland in Colorado. *J. Range Manage.* 21:203-208.
- Stewart, C., and A. C. Hull. 1949. Cheatgrass, (*Bromus tectorum* L. - an ecological intruder in southern Idaho. *Ecol.* 30:58-74.
- Uresk, D. W. 1978. Diets of the black-tailed hare in steppe vegetation. *J. Range Manage.* 31:439-442.
- Westoby, M., and F.H. Wagner. 1973. Use of a crested wheatgrass seedling by black-tailed jackrabbits. *J. Range Manage.* 26:349-352.

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Dale L. Nolte,¹ U.S. Department of Agriculture, Animal and Health Inspection Service, Denver Wildlife Research Center, 1835 Black Lake Blvd. S.W., Olympia, Washington 98512

Gisela Eppele, Monell Chemical Senses Center, 3500 Market Street, Philadelphia, Pennsylvania 19104-3308

Dan L. Campbell, U.S. Department of Agriculture, Animal and Health Inspection Service, Denver Wildlife Research Center, 1835 Black Lake Blvd. S.W., Olympia, Washington 98512

and

J. Russell Mason, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Denver Wildlife Research Center, c/o Monell Chemical Senses Center, 3500 Market Street, Philadelphia, Pennsylvania 19104-3308

Response of Mountain Beaver (*Aplodontia rufa*) to Conspecifics in Their Burrow System

Abstract

The role of chemical communication in the social behavior of most burrowing rodents is largely unknown. We constructed artificial burrow systems to study interactions between mountain beavers (*Aplodontia rufa*). Though beavers exhibited scent marking behaviors, the marks did not prevent intruders from entering and exploring burrow systems. Encounters were agonistic and resident animals aggressively evicted intruders. We speculate that scent marking enhances the territorial confidence of the established mountain beaver.

Introduction

Mountain beavers (*Aplodontia rufa*) are generally regarded as a primitive fossorial rodent. Endemic to the Pacific Northwest, its range is associated with high rainfall and edaphic conditions that promote succulent vegetation and humid burrows (Voth 1968). The limits to their geographic distribution, however, are probably dictated by thermal requirements and adequate soil drainage, rather than forage availability (Beier 1989).

Burrow systems of mountain beaver have multiple openings and chambers and occur at any depth from beneath forest debris to 2 m below the surface (Feldhamer and Rochelle 1982). Chambers are used for nesting, food caches and fecal/refuse deposits (Voth 1968). Nest and feeding chambers form a hub from which burrows and other chambers radiate (Martin 1971). Nest chambers (50-60 cm diameter and 30-40 cm high) are packed with vegetation in which the animal constructs a small centrally located nest (Martin 1971). Food caches are stored in nearby chambers of similar or smaller size. Fecal/refuse chambers are generally located within a few meters (1-3) of the nest (Voth 1968). These vary in size and construction from blind tunnels to chambers larger than the nest chamber.

Mountain beavers travel through interconnecting burrows to forage (Martin 1971). Forays outside their burrow system are primarily nocturnal and generally within the proximity of a burrow entrance (Ingles 1959). Clipped plants are dragged or carried back to the burrow (Voth 1968).

Home ranges of mountain beavers often overlap and animals frequently share interconnecting runways (Martin 1971, Lovejoy and Black 1979). Nest and associated burrows, however, are the domain of an individual animal. Established animals rarely travel beyond their home ranges which vary in size from 0.03-0.2 ha. Dispersing subadults, however, may travel extensively, moving above-ground as well as through existing burrows (Martin 1971). Adult males may also extend their movements during the breeding season.

The role of chemical communication in the social behavior of mountain beavers is mostly unknown (Brown 1985). The only reported incidence of scent marking is of a captive male that marked a territory with urine (Wandeler and Pilleri 1965). The use of scent marks, however, would not be surprising. Although solitary, mountain beavers often live close to conspecifics (Lovejoy and Black 1979, Neal and Borrecco 1981). Territorial marking for defensive purposes might be expected because established nest sites appear to be a valuable resource to mountain beavers. Nests are rarely vacated voluntarily (Martin 1971), and nests which

¹Post-doctoral fellow with the Monell Chemical Senses Center at the time of the study.

do become available are quickly occupied by other mountain beavers (Campbell *et al.* 1988).

We report the responses of resident mountain beaver to conspecific intruders encountered in an artificial burrow system. To our knowledge, this is the first description of encounters between these animals in a naturalistic setting.

Materials and Methods

Subjects

Mountain beavers were live trapped in the Capitol State Forest, Grays Harbor County, approximately 30 km from Olympia, Washington during July and August, 1991. After a minimum of 2 weeks habituation to captivity, animals that weighed >800 g when captured were air-shipped to the Monell Chemical Senses Center, Philadelphia, Pennsylvania. On arrival at Monell, all mountain beavers were given 14 days to adjust and establish a nest. Animals were individually caged (92 x 62 x 50 cm) under a changing light:dark cycle that reflected the natural day:night cycle of Olympia, Washington. Animals not involved in trials were maintained in these cages. Individual cages also consisted of an outside detachable bucket (30 cm dia. x 27 cm), used by mountain beavers as a nest. Access to this bucket was through a PVC pipe (15 cm dia. x 15 cm), which could be blocked by a sliding panel to lock animals in their nest. Aspen shavings (#1019; Buckshire Feeds, LTD, Lansdale, PA) spread on the cage floor were carried into the bucket by the resident mountain beaver for nesting material. Mountain beavers had free access to water and a 70:30 mixture of omnivore pellets and guinea pig food (RP 5635 Purina - Mozuri Zoo Feed "A" Omnivore and RP 5025 Purina - Guinea Pig Checkers, respectively; Buckshire Feeds LTD, Lansdale, PA). Slices of apple were also given to the animals 2 or 3 times a week.

Artificial Burrow System

Two burrow systems (Figure 1a) were constructed to monitor mountain beaver activity. Each system consisted of an open cage (204 x 92 x 64 cm) with an assortment of tunnels and chambers below (Figure 1b). Burrows were constructed of clear PVC pipe (15 cm dia.) and chambers consisted of polyethylene buckets (30 cm dia. x 27 or 35 cm) with plexiglass windows in the lids. Free access to food and water was provided in the open cage and aspen shavings covered the cage floor.

Mountain beavers to be introduced to the artificial burrow system were first secured in the detachable nest bucket attached to their individual cage. This nest bucket was then attached to the artificial burrow system (B-4; Figure 1b). Thus, each introduced mountain beaver had the option to retreat to its own established nest.

Procedure

Interactions between mountain beavers were observed in the morning at the beginning of the light period. Trials were concluded when animals returned to their respective nests and failed to emerge again for 15 min. Encounters were always between animals unfamiliar with each other. An intruder was never reintroduced to a system if it had previously encountered the resident animal.

A female mountain beaver was initially placed in each burrow system and allowed 48 hours to explore and establish a territory. Over the next 30 days, female (5) and male (13) mountain beavers were introduced into these occupied systems. Only one intruder was allowed to invade at a time and a minimum of 24 hours elapsed between encounters. After these initial tests the resident females were replaced with males. These males were allowed 48 hours to establish themselves and then we observed their response to an invading naive female. The original female occupant of each system was then reintroduced (72 hours after being replaced with a male). Initial encounters with the current male occupants were observed and then for 60 days we monitored animal and nest locations. This 60 day period overlapped the normal breeding season for mountain beaver. Finally, male occupants of each burrow system were removed and the females were observed for another 90 days.

Results and Discussion

When introduced to an unoccupied system, mountain beavers invariably vacated their attached nests and established residency in an artificial system. Subsequent animals readily accepted the nest and fecal chambers established by the original occupants. Though animals explored and exploited vacated systems, introduced mountain beavers never replaced a resident animal.

Mountain beaver responses to invading conspecifics in their burrow systems were always agonistic. Except for one male's intermittent acceptance

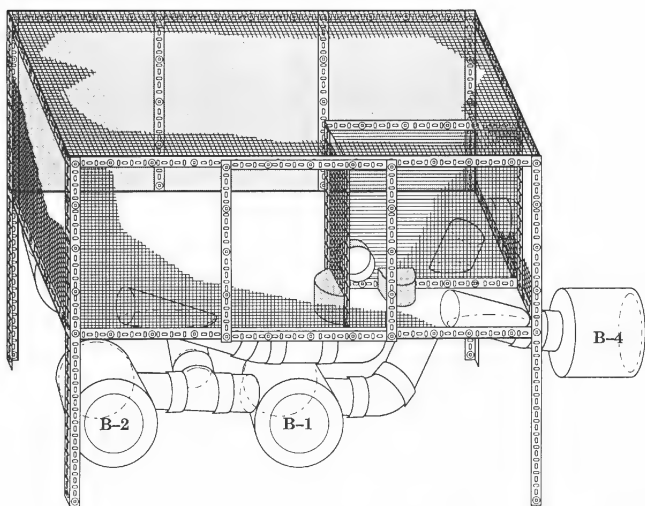


Figure 1a

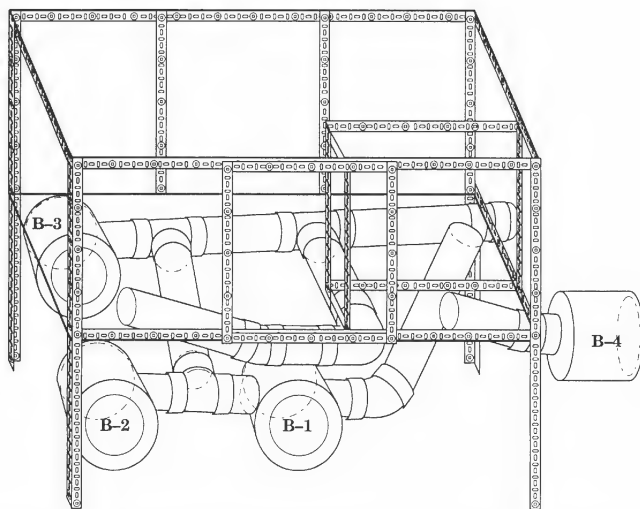


Figure 1b

Figure 1. Artificial burrow system constructed to resemble the solitary chambers and associated burrows of a mountain beaver. Systems consisted of an open cage (Figure 1a) and an assortment of tunnels and chambers below (Figure 1b).

of a female over a 3 day period during the breeding season, intruders were aggressively evicted by the resident animal. These observations are consistent with studies of mountain beaver under natural conditions which report nest sites to be occupied by a single animal (Martin 1971, Lovejoy and Black 1979). Aggressive behavior, however, appeared to be limited to the burrow system. Our artificial systems were small relative to a mountain beaver's home range; therefore, it was not pos-

sible to determine the response of mountain beavers to conspecifics in burrows outside the immediate vicinity of nests. However, mountain beavers that met outside the system ignored one another and resident animals never attempted to protect the food or water source on the surface. Mountain beavers introduced simultaneously in enclosures (1 ha) are not agonistic towards each other and initially may even share a nest (unpubl. data). Wild mountain beavers often travel the same

interconnecting runway system (Martin 1971, Lovejoy and Black 1979). The nature of encounters among animals along these runways is unknown.

Mountain beavers appeared to mark burrows outside their nest with odors, a behavior that might be expected from solitary animals that live in close proximity to conspecifics. Additionally, territorial marking in mammals is almost universally linked to agonistic behavior (Gosling 1990).

Rodents use urine, feces, specialized scent glands and vaginal secretion for chemical communication (Brown 1985). Mountain beaver may mark territories with secretions from sebaceous glands. Sebaceous gland secretions collect in hair follicles of the oral angle and lips (Quay 1965). Mountain beavers alternated between grooming and rubbing against chamber entrances and burrows, and while grooming they frequently put their feet to their mouths. Subsequently, marked areas were repeatedly sniffed by both the intruder and established animal. Several sciurid species (e.g. *Spermophilus* spp., *Tamias* spp.) use oral secretions from sebaceous glands for scent marking (Quay 1965).

Mountain beavers also produce a white secretion from the harderian and lacrimal glands near their eyes during some stressful situations (Hackman *et al.* 1990). In our study, white eye secretion was observed only on intruders when nose to nose with the resident animal. Animals that exhibited the secretion appeared frozen in place. This secretion may induce a tonic immobility, an adaptive defence reaction to attack (Hackman *et al.* 1990). Tonic immobility eliminates the movement stimuli that elicits an attack (Thompson *et al.* 1981), yet allows the animal to monitor its environment (Ewell *et al.* 1981). The secretion may also serve a semiochemical function. Secretion on the vibrissae may passively impart information about burrow usage (Hackman *et al.* 1990). Perhaps a submissive cue is passed to the aggressor.

Though mountain beaver marked burrows with scents these marks were not sufficient to prevent invasion by conspecifics. Intruders repeatedly explored occupied systems, rapidly exploiting any opportunity to establish themselves. Further, invaders left established nests of their own to occupy a nest recently abandoned by another animal. This continuous explorative and exploitive behavior may be

reflective of similar behavior practiced by wild animals. An established female is reported to have traveled over 80 m to occupy the nest of a deceased male (Martin 1971). Additionally, extensive areas (40 ha) in which all mountain beaver have been removed are quickly invaded by other mountain beaver unless vacated nests are destroyed (Campbell *et al.* 1988).

Scent marking may serve to enhance the territorial confidence of mountain beaver. Established animals invariably retained possession of the burrow system and familiarity does not fully explain this dominance. Males ejected females after living in a burrow system for only 72 hours. Even though the ejected females had occupied the same system for 30 days and only 72 hours earlier had successfully evicted the current male. Established and intruding animals stopped to investigate marked areas. Recognition of odors may have enhanced the confidence of the established animal while weakening that of the intruder. Territorial confidence of European wild rabbits (*Oryctolagus cuniculus*) increases in the presence of odors from their scent glands (Mykytowycz *et al.* 1976). Presence of a rabbit's odor on otherwise neutral ground during encounters between rabbits generally dictates the dominant animal. Chin secretions are the most effective odor to stimulate confidence.

These observations provide some insight into the intra-specific encounters of mountain beavers in a naturalistic setting. Resident mountain beavers exhibited scent marking behaviors, however, these marks did not prevent intruders from entering and exploring a burrow system. Rather a vacated nest was quickly accepted by an intruding mountain beaver as its own. Occupied systems, however, were protected by the resident animals and encounters close to their nest were agonistic and the intruder aggressively evicted.

Acknowledgements

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Literature Cited

- Beier, P. 1989. Use of habitat by mountain beaver in the Sierra Nevada USA. *J. Wildl. Manage.* 53:649-654.
- Brown, R. E. 1985. The rodents II: suborder Myomorpha. In R. E. Brown, and D. W. MacDonald (eds.) *Social Odours In Mammals*. Clarendon Press, Oxford. Vol. 1, Pp. 345-457.
- Campbell, D. L., J. D. Ocheltree, and M.G. Carey. 1988. Adaptation of mountain beaver (*Aplodontia rufa*) to removal of underground nests. *Northw. Sci.* 62:75.
- Ewell, A. H., P. K. Rudeen, and W. K. O'Steen. 1981. Tonic immobility as a predator defense in the rabbit (*Oryctolagus cuniculus*). *Behav. Neural Biol.* 31:483-489.
- Feldhamer, G. A., and J. A. Rochelle. 1982. Mountain beaver—*Aplodontia rufa*. In J. A. Chapman, and G. A. Feldhamer (eds.) *Wild Mammals of North America*. John Hopkins University Press, Baltimore and London. Pp. 167-175.
- Gosling, L. M. 1990. Scent marking by resource holders: alternative mechanisms for advertising the costs of competition. In D. W. MacDondald, D. Muller-Schwarze and S. E. Natynczuk (eds.) *Chemical Signals in Vertebrates 5*. Oxford University Press, New York. Pp. 315-328.
- Hackman, N., C. S. Zamora, and E. Stauber. 1990. The white eye secretion in *Aplodontia*. In D. W. MacDondald, D. Muller-Schwarze, and S. E. Natynczuk (eds.) *Chemical Signals in Vertebrates 5*. Oxford University Press, New York. Pp. 141-146.
- Ingles, L. G. 1959. A quantitative study of mountain beaver activity. *Am. Midl. Nat.* 61:419-423.
- Lovejoy, B. P., and H. C. Black. 1979. Movements and home range of the pacific mountain beaver *Aplodontia rufa pacifica*. *Am. Midl. Natl.* 101:393-402.
- Martin, P. 1971. Movements and activities of the mountain beaver *Aplodontia rufa*. *J. Mammal.* 52:717-723.
- Mykirowycz, R., E. R. Hesterman, S. Gambale, and M. L. Dudzinski. 1976. A comparison of the effectiveness of the odors of rabbits, *Oryctolagus cuniculus*, in enhancing territorial confidence. *J. Chem. Ecol.* 2:13-24.
- Neal, F. D., and J. E. Borrecco. 1981. Distribution and relationship of mountain beaver *Aplodontia rufa* to openings in sapling stands. *Northw. Sci.* 55:79-86.
- Quay, W.B. 1965. Comparative survey of sebaceous and sudoriferous glands of the oral lips and angle in rodents. *J. Mammal.* 46:23-37.
- Thompson, R. K. R., R. W. Foltin, R. J. Boylan, A. Sweet, C. A. Graves, and C. E. Lowitz. 1981. Tonic immobility in Japanese quail can reduce the probability of sustained attack by cats. *Anim. Learn. Behav.* 9:145-149.
- Voth, E.H. 1968. Food habits of the Pacific mountain beaver, *Aplodontia rufa pacifica*. Oregon State University, Corvallis. Ph.D. Dissertation.
- Wandeler, I., and G. Pilleri. 1965. Weitere beobachtungen zum verhalten von *Aplodontia rufa rafinesque* (Rodentia, Aplodontioidea) in gefangenschaft. *Z. Tierpsychol.* 22:570-583.

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Comparison of Rumen and Fecal Analysis to Estimate Moose Diets

Abstract

Large ungulate management and research projects often require estimates of diet composition, and indirect methods are often the only feasible alternatives. We compared diet estimates based on moose (*Alces alces gigas*) rumen and fecal samples taken from the same animal on the Copper River Delta, Alaska. Twenty-five animals were sampled, the majority of which were killed by hunters during September. Three procedures were used, a standard microhistological technique on both rumen and fecal samples and a macroscopic technique on rumen samples. The macroscopic analysis of rumen samples identified contents to species and specific plant parts. However, the results of macroscopic rumen analysis can be affected by seasonal changes in rumen particle size. Microhistological analysis of both rumen and fecal samples could not differentiate among willow species (*Salix* spp.), the dominant food item, nor could plant parts be distinguished. These are major shortcomings of this procedure. However, when willows were identified only to genus, diets estimated by the 3 procedures differed ($P < 0.001$) only for minor items ($< 5\%$ of the diet), or items that were unidentifiable microhistologically (i.e., wood fragments, catkins). Quantifying rumen and fecal winter samples was difficult. Each procedure had shortcomings, and a combination of procedures may have to be used, particularly if study objectives require large sample sizes from a variety of individual animals. Knowledge of the strengths and weaknesses of diet estimation procedures allows investigators to assess methods in relation to project objectives and when evaluating the results of other studies.

Introduction

Estimates of diet composition for large ungulates are basic to many management programs and research efforts. A variety of methods are potentially available and information on the magnitude and direction of relative bias for each technique would be valuable in project planning and in assessing data on diet composition.

Moose occur in most regions of Alaska and inhabit a variety of habitat types that differ in forage species composition, abundance, and quality (LeResche *et al.* 1974). However, information on the diets of moose in Alaska is limited to the Kenai Peninsula (LeResche and Davis 1973, Cushwa and Coady 1976, Regelin *et al.* 1987a), Fairbanks and vicinity (Cushwa and Coady 1976), Denali National Park (Risenhoover 1989, Van Ballenberghe *et al.* 1989, Miquelle *et al.* 1992), and a small population in southeast Alaska (Doerr *et al.* 1980).

This information gap is probably due to a number of factors including lack of confidence in some techniques (Regelin *et al.* 1987b). Moose forage selection in Alaska has been inferred from browse surveys (Peek 1974) and indirectly estimated from rumen samples (Cushwa and Coady 1976, Doerr *et al.* 1980) or fecal samples (Regelin *et al.*

1987b). In addition, direct observation of tame-habituated animals (LeResche and Davis 1973, Regelin *et al.* 1987a, Risenhoover 1989) or a combination of techniques (Van Ballenberghe *et al.* 1989, MacCracken 1992) have been used.

The most accurate method of estimating the diets of moose is probably the bite-count technique, where results are expressed as mass of dry matter ingested. However, this method is extremely labor intensive and requires that tame or habituated animals be available. For most management and research projects, rumen and fecal analyses are the methods commonly used. The availability of rumen samples can be limited and skewed by seasonal mortality patterns, but fecal samples are potentially widely available.

The purpose of this study was to compare diet estimates derived from the analysis of paired rumen and fecal samples of moose on the Copper River Delta, Alaska.

Study Area and Methods

Rumen and fecal samples were collected from moose on the Copper River Delta (CRD) in south-central Alaska. The CRD is immediately east of Prince William Sound and encompasses about 3,200 km². MacCracken (1992) described the study area in detail, the habitat types important to moose, and other aspects of moose ecology on the CRD.

¹Present address: Policy Analysis Group, College of Forestry, Wildlife, and Range Sciences, University of Idaho, Moscow, Idaho 83843.

Samples for this study came from the west CRD (WCRD) subpopulation during 1987-1989. Samples were collected by hunters and project personnel. Twenty-five paired rumen and fecal samples were examined in this study. Nineteen of the samples were collected during the hunting season. The remainder were collected in October (2), November (2), and 1 each in February and May.

Moose rumens were sampled by taking 4 subsamples from each quarter of the rumen-reticulum complex. A handful of material constituted a subsample and the subsamples were combined in a plastic bag, making an approximate 1-2 L sample. A 0.25-0.5 L fecal sample was taken directly from the rectum. Both rumen and fecal samples were oven-dried at 60°C for 48 h for storage.

The rumen samples were analyzed using 2 procedures. First, a macroscopic examination (rumen-macro) of the contents was conducted (Zach *et al.* 1982). The dried rumen samples were soaked in water for ≥ 48 h then washed through a series of sieves. Material that accumulated in a sieve with a 4-mm opening was air dried then spread onto a white enamel tray that was marked with a grid system delineating 100 cells that were 8 cm² each. Thirty of the 100 cells were selected at random and the contents identified to species-part with the aid of a dissecting microscope (10 x power). The identified material was dried at 60°C for 48 h then weighed to the nearest 0.01 g. A percent dry weight for each species-part was calculated for each sample. The identified material was then added to the contents remaining on the tray, and the remainder of the rumen sample that had passed through the 4-mm mesh sieve and collected in a 2-mm mesh sieve.

The recombined rumen samples were then analyzed microhistologically (rumen-micro). The samples were ground in a Wiley mill to pass through a 1-mm mesh screen. A portion of the ground material for each sample was made into 5 microscope slides and 20 fields/slide examined for identifiable plant fragments. A valid field had at least 2 identifiable plant fragments and an identifiable plant fragment had at least 2 unique characteristics. Plant fragments were identified to the lowest taxonomic level possible, most often genus, and frequently species. Each slide was a subsample and the counts of identifiable plant fragments/100 fields were quantified as percent relative density, a close

approximation to percent dry weight (Sparks and Malechek 1968). The fecal samples were also analyzed microhistologically following the same procedures.

This analysis assumed that moose diets did not change significantly between the meal(s) represented by the feces and the rumen. Schwartz *et al.* (1988) reported total mean retention times of liquid ingesta by moose of 38 and 54 h for high and low quality diets, respectively. Hubbert (1987) reported a high correlation between passage rates of liquid and particulate ingesta in moose. Hanley *et al.* (1985) conducted a similar analysis with Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) and stated that constant forage selection a week prior to sampling was assumed. Significant changes in the diets of moose on the WCRD occurred during April-May, July, and November (MacCracken 1992). Based on these facts, the assumption of constant diet composition was likely met for a majority of samples analyzed in this study.

The samples were not independent which violated a major assumption of most statistical tests. However, our objective was to assess the variation among diet estimation techniques which was most accurately determined with dependent samples.

Two questions were addressed. The first was whether there were any significant differences in diet composition estimated by the 3 procedures. This was examined with a 2-way MANOVA, blocking on individual animals. Due to the preponderance of estimates $\geq 80\%$ and $\leq 5\%$ in the data matrix, percentages were converted to ranks prior to analysis (Conover and Iman 1981, K. Steinhorst, pers. commun., 1991). The canonical structure of the MANOVA model was examined to determine which diet items were responsible for any differences (SAS Inst., Inc. 1988).

The second question considered the degree of association among the procedures. This was assessed by plotting the data for comparisons between the rumen-macro analysis and the rumen-micro and fecal analyses. We assumed that rumen-macro estimates were closest to the true diet, since most material could be positively identified and differential digestion of plant species would be minimal. Four forage categories were evaluated in this analysis: willows, other browse, total forbs, and total graminoids. A least squares regression line was estimated and plotted for each comparison.

Results and Discussion

The twigs and leaves of Barclay willow (*S. barclayi*) were the most abundant items identified by the rumen-macro procedure (35% and 42%, respectively). Willow twigs that could not be identified to species were the next most abundant item (23%), followed by Sitka alder (*Alnus sinuata*) leaves (9%), sweetgale (*Myrica gale*) twigs (8%), wood fragments (5%) and sweetgale leaves and willow catkins (3% and 2%, respectively).

Rumen-micro and fecal procedures could not distinguish among species of willow or specific plant parts. Thus, statistical comparisons among the 3 procedures were made by lumping willows and not differentiating plant parts.

There were significant differences ($F = 4.1$, $P = 0.0001$) in diet estimates among the 3 procedures (Table 1). However, these differences occurred only for items that were a minor portion of the diet (i.e., *Epilobium* spp., *Populus trichocarpa*), or plant parts that were unidentifiable microhistologically (i.e., wood fragments, catkins). Estimates

of other items in the diets were not different ($P > 0.05$) among the 3 procedures. There were also significant differences among animals ($F = 1.25$, $P = 0.02$), but again, these were attributed to estimates of relatively minor items (i.e., *Epilobium* spp., *Equisetum* spp., and *Carex* spp.).

Results of the regression analyses were variable. For willows, fecal estimates were closest to rumen-macro estimates (Figure 1). This relationship was also true for forbs (Figure 2). However, for the other browse and graminoid categories, the two rumen estimates produced the closest results (Figures 3 and 4). This inconsistency has no apparent explanation. We would have predicted that estimates from fecal samples would have consistently deviated the most from the rumen-macro estimates due to differential digestion of plants, variable passages rates, and greater amounts of unidentifiable material in feces (Gill *et al.* 1983).

TABLE 1. Mean (SE) percent of items identified in paired rumen and fecal samples of moose on the west Copper River Delta, Alaska.

Item	Rumen ^a		Fecal
	Macro	Micro	
<i>Alnus sinuata</i>	3(1)	1(0.4)	2(1)
<i>Myrica gale</i>	3(2)	2(0.3)	3(1)
<i>Populus trichocarpa</i>	1(1)	1(0.2)	1(0.1)
<i>Salix</i> spp.	83(4)	86(4)	90(2)
Total browse	90(4)	90(4)	96(1)
<i>Epilobium</i> spp.	1(1)	*	*
<i>Equisetum</i> spp.	1(0.3)	2(1)	1(0.4)
Total forb	3(1)	3(1)	2(0.1)
<i>Calamagrostis</i> spp.	*	1(1)	*
<i>Carex</i> spp.	2(2)	1(1)	*
<i>Eriophorum</i> spp.		1(1)	1(0.4)
Unidentified graminoid	1(0.3)	1(0.1)	*
Total graminoid	3(2)	3(2)	2(1)
Lichen	1(1)	*	
Catkin	2(2)		
Wood fragment	5(2)		

^aRumen samples were analyzed macroscopically and microhistologically. Fecal samples were analyzed microhistologically.

* < 1%.

SALIX SPP.

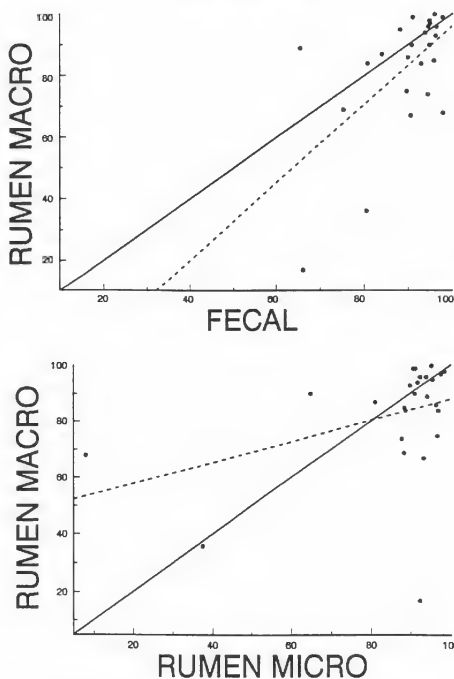


Figure 1. Plots of percent willows (*Salix* spp.) in moose rumen and fecal samples. The solid line is the 1:1 relationship. The dashed line is the least squares regression.

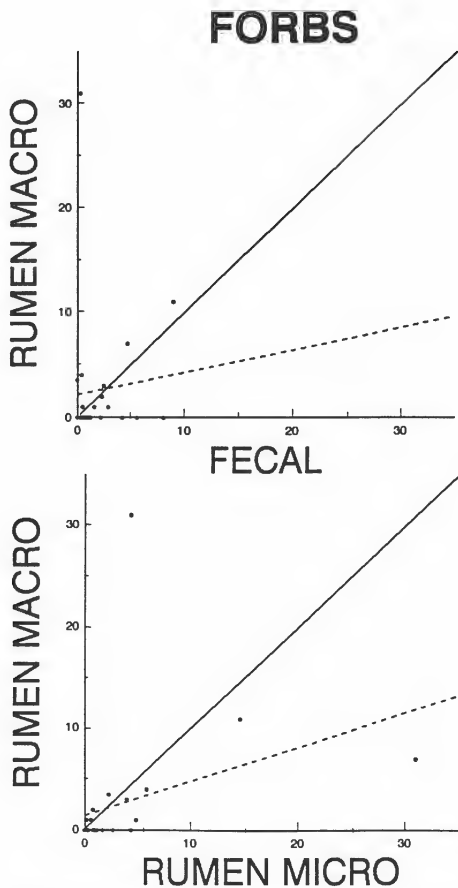


Figure 2. Plots of percent forbs in moose rumen and fecal samples. The solid line is the 1:1 relationship. The dashed line is the least squares regression.

Overall, agreement among the 3 procedures was greatest for graminoids, followed by willows, other browse, then forbs. These results were as expected based on the known biases of each procedure (Westoby *et al.* 1978, Vavra and Holecheck 1980, Hanley *et al.* 1985).

Despite close agreement for major diet components, each procedure had shortcomings. Rumen and fecal-micro procedures could not identify willows to species and could not identify specific plant parts. These traits are a major limitation of this procedure when applied to moose samples since willows are the primary diet item in many areas, numerous species of willow are often available, and moose preferentially forage on some species

(Risenhoover 1987). However, fecal analysis in combination with direct observations of foraging moose (Van Ballenberghe *et al.* 1989), examination of feeding sites, and browse surveys (Peek 1974, MacCracken 1992) may reasonably estimate the relative importance of willows and seasonal trends in use as well as preferences for species and plant parts.

The rumen-macro procedure can be affected by choice of sieve size in the preparation of samples. Nygren and Hoffman (1990) reported that the average rumen particle size in moose changed with forage digestibility and rumen retention time from approximately 2 mm in winter samples to ≥ 4 mm in summer samples. Additionally, we observed numerous fragments of horsetail (*Equisetum* spp.) passing through the 4-mm mesh sieve, suggesting that particle size also varies among plant species and may be related to cell wall structure and fracture characteristics. These results suggest that the analysis of rumen samples should use a 2-mm mesh sieve.

Winter diets of moose were difficult to estimate with either rumen or fecal samples. The February rumen sample examined in this study was dominated by relatively large fragments of wood devoid of identifying characteristics. This was typical of moose rumen contents in winter and was probably the source of some of the problems reported by Regelin *et al.* (1987b:263), i.e., "trashy" samples with lots of unidentifiable material. In addition, we relaxed the criteria defining an identifiable fragment and a valid field to 1 characteristic/fragment, and 1 fragment/field for the microhistological analysis of winter rumen and fecal samples.

Our results support Peek's (1974) conclusion that a variety of procedures may be needed to estimate moose diets. For studies having objectives that require replicated sampling from a large number of animals, fecal analysis is probably the only method that can meet those goals (Hanley *et al.* 1985). The biases associated with fecal analysis have been thoroughly examined (Holecheck 1982, Gill *et al.* 1983, Holecheck and Valdez 1985, Vavra and Holecheck 1980, Hinnant and Kothmann 1988) and can be partially overcome by incorporation of the results of other methods. We found relatively good agreement between fecal and rumen analyses, and Van Ballenberghe *et al.* (1989) reported similar results for fecal analysis and bite-count methods during summer. These conclusions suggest that investigators can confidently use fecal analysis to estimate trends in

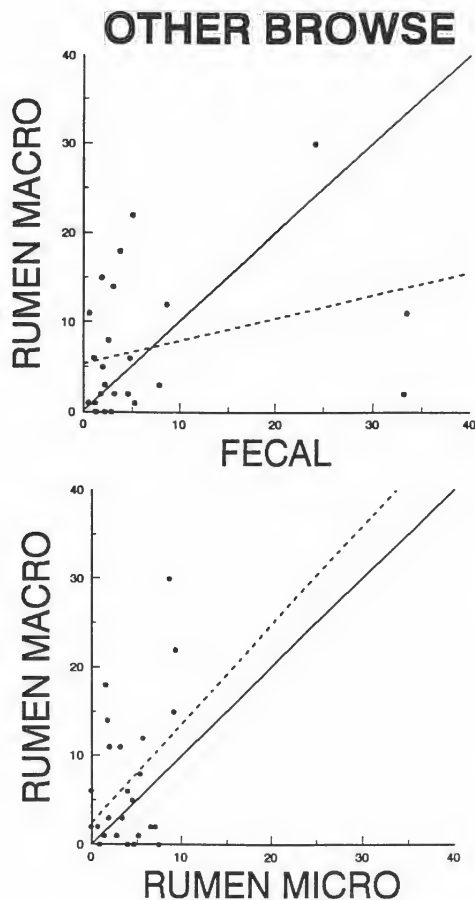


Figure 3. Plots of percent browse, excluding willows (*Salix* spp.), in moose rumen samples and fecal samples. The solid line is the 1:1 relationship. The dashed line is the least squares regression.

willow consumption and the relative importance of willows in the diet, realizing that winter diets and details on species and plant part selection during any season will have to be assessed using other methods.

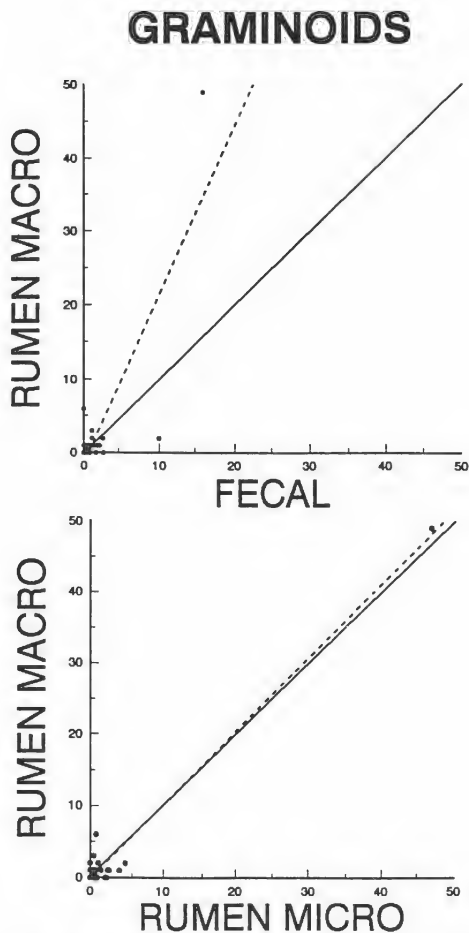


Figure 4. Plots of percent of graminoids in moose rumen and fecal samples. The solid line is the 1:1 relationship. The dashed line is the least squares regression.

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Literature Cited

- Conover, W. J. and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Amer. Statistician* 35:124-129.
- Cushwa, C. T. and J. Coady. 1976. Food habits of moose, *Alces alces*, in Alaska: a preliminary study using rumen contents analysis. *Can. Field-Nat.* 90:11-16.
- Doerr, J. G., E. L. Young, and A. W. Franzmann. 1980. Ecological and physiological aspects of a moose population in Thomas Bay, southeast Alaska. *N. Amer. Moose Conf. Workshop.* 16:203-237.
- Gill, R. B., L. H. Carpenter, R. M. Bartmann, D. L. Baker, and G. G. Schoonveld. 1983. Fecal analysis to estimate mule deer diets. *J. Wildl. Manage.* 47:902-915.
- Hanley, T. A., D. E. Spalinger, K. A. Hanley, and J. W. Schoen. 1985. Relationships between fecal and rumen analyses for deer diet assessments in southeastern Alaska. *Northwest Sci.* 59:10-16.
- Hinnant, R. T. and M. M. Kothmann. 1988. Collecting, drying, and preserving feces for chemical and microhistological analysis. *J. Range Manage.* 41:168-171.
- Holecheck, J. L. 1982. Sample preparation techniques for microhistological analysis. *J. Range Manage.* 35:267-268.
- Holecheck, J. L., and R. Valdez. 1985. Magnification and shrub stemmy material influence on fecal analysis accuracy. *J. Range Manage.* 38:350-352.
- Hubbert, M. E. 1987. The effect of diet on energy partitioning in moose. University of Alaska, Fairbanks. Ph.D. Thesis.
- LeResche, R. E., R. H. Bishop, and J. W. Coady. 1974. Distribution and habitats of moose in Alaska. *Nat. Can. (Que.)* 101:143-178.
- LeResche, R. E., R. H. Bishop, and J. L. Davis. 1973. The importance of nonbrowse foods to moose on the Kenai Peninsula, Alaska. *J. Wildl. Manage.* 37:279-287.
- MacCracken, J. G. 1992. Ecology of moose on the Copper River Delta, Alaska. University of Idaho, Moscow. Ph.D. Thesis.
- Miquelle, D. G., J. M. Peek, and V. Van Ballenberghe. 1992. Sexual segregation in Alaskan moose. *Wildl. Monogr.* 122.
- Nygren, K., and R. R. Hofmann. 1990. Seasonal variations of food particle size in moose. *Alces* 26:44-50.
- Peek, J. M. 1974. A review of moose food habits studies in North America. *Nat. Can. (Que.)* 101:195-215.
- Regelin, W. L., C. C. Schwartz, and A. W. Franzmann. 1987a. Effects of forest succession on nutritional dynamics of moose forage. *Swedish Wildl. Res. Suppl.* 1:247-263.
- Regelin, W. L., M. E. Hubbert, C. C. Schwartz, and D. J. Reed. 1987b. Field test of a moose carrying capacity model. *Alces* 23:243-284.
- Risenhoover, K. L. 1987. Intraspecific variation in moose preference for willows. *In* F. D. Provenza, J. T. Flinders, and E. D. McArthur (eds.) *Proceedings-symposium on plant-herbivore interactions*. U.S.D.A. For. Serv., Gen. Tech. Rep. INT-222. Pp. 58-63.
- . 1989. Composition and quality of moose winter diets in interior Alaska. *J. Wildl. Manage.* 53:568-577.
- SAS Institute, Inc. 1988. *SAS/STAT user's guide*, release 6.03 edition. SAS Inst. Inc., Cary, North Carolina.
- Schwartz, C. C., W. L. Regelin, A. W. Franzmann, R. G. White, and D. F. Holleman. 1988. Food passage rate in moose. *Alces* 24:97-101.
- Sparks, D. R. and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscope technique. *J. Range Manage.* 21:264-265.
- Van Ballenberghe, V., D. G. Miquelle, and J. G. MacCracken. 1989. Heavy utilization of woody plants by moose during summer at Denali National Park, Alaska. *Alces* 25:31-35.
- Vavra, M., and J. L. Holecheck. 1980. Factors influencing microhistological analysis of herbivore diets. *J. Range Manage.* 33:371-374.
- Westoby, M., C. R. Rost, and J. A. Weis. 1976. Problems with estimating herbivore diets by microscopically identifying plant fragments from stomachs. *J. Mammal.* 57:167-172.
- Zach, R., V. F. J. Crichton, J. M. Stewart, and K. R. Mayoh. 1982. Early winter food habits of Manitoba moose as determined by three rumen analysis methods. *Can. J. Zool.* 60:1300-1304.

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Effects of Race-day Weather and Topographic Severity on Performance in Duathlon Races: Inter-race Comparisons from the Pacific Northwest

Abstract

We examined the influence of race-day weather and topographic variability of courses on performance of male athletes in a series of duathlon (run-bike-run) competitions held in Oregon and British Columbia. Subtraction matrices and ANOVA techniques are used to identify unique races and performance patterns among races. Enhanced or reduced performance in the overall race and individual race segments is then related to topographic severity of the courses and environmental conditions encountered by the athletes during the races. Results suggest that variations in race-day weather conditions have only a minor impact on performance. Topographic severity of individual race segments and the cumulative effects of topographically difficult races are the dominant controls of performance. Results from this study offer a scientific basis for race directors and organizers to develop a range of duathlon courses that can significantly enhance or reduce performance.

Introduction

The Pacific Northwest region of the United States and Canada has seen an increase in multi-sport competitions from the late-1980's until the present. Duathlon, the most recent addition, provides a new alternative for multi-sport enthusiasts looking for a complement to the triathlon (swim-bike-run event). The sport typically has three separate segments, usually in order of running, bicycling, and running with no rest periods between each segment. The most common and popular race has been the 5km run, 30km bicycle, and 5km run international duathlon (Graham 1990; Newkirk 1989).

Although there is a paucity of research on duathlons, examination of the swim, bicycle, and run segments of the triathlon is useful to duathlon researchers. Recent studies have emphasized the physiological (Kohrt *et al.* 1987; Kreider *et al.* 1988; Loftin *et al.* 1988) and medical (Hiller *et al.* 1987; Hiller 1989) aspects of the triathlon. Triathlon performance has been correlated with VO_{2max} , the maximum volume of oxygen an individual can use (uptake) (Kohrt *et al.* 1987; Kreider *et al.* 1988; Loftin *et al.* 1988), and cardiovascular/thermal responses (Kreider *et al.* 1988). Kohrt *et al.* (1987) found that VO_{2max} was significantly related to bicycling and running performance in a triathlete. Hiller *et al.* (1987) examined medical records for triathlons of various lengths and found the most common medical problems to be dehydration and heat exhaustion.

The effects of weather on performance in run-only events is much better understood (Costill 1972; Pugh 1974; Davies 1980; England *et al.* 1982). Both Pugh (1974) and Davies (1980) examined the effects of wind resistance on runners and found there is an increase in oxygen uptake (i.e. increasing stress) by athletes running in middle distance track events with increasing wind speed. Cross winds were also responsible for affecting performance in some middle distance runners (Davies 1980). Heat exhaustion and heat stroke are commonly encountered problems among competitors during high temperature and humidity conditions, as this combination tends to impair evaporative cooling.

In an analysis of the physiology of marathon runners, Costill (1972) suggested that environment and course topography may drastically influence marathon performance. Eyton (1987) examined a multi-stage, long-distance road race and found the most significant variables for performance were stage distance and the uphill component of the stage. Energy expenditure and run performance times of simulated orienteering conditions were compared on flat and hilly routes by Knowlton *et al.* (1988). They found that the same length route with a short, steep incline required less energy than a route with a longer, more gradual incline.

Because the first official duathlon took place less than ten years ago (1984), there has been a limited amount of research on inter-race variability in performance and the potential limiting factors

of performance. The primary purpose of this study is to examine how topographic variation and race-day weather affects the level of performance in male "middle-of-the-pack" (MMP) duathletes. Guiding research questions are: 1) what influences do variations in race course topography and race-day weather have on mean final race times among a sample of races based on a standard duathlon course of a 5km first run, 30km bicycle portion, and a 5km second run, and 2) how do the average split times (times for individual race segments) vary among races and are they a good indicator of the influence of course difficulty and atmospheric conditions on MMP performance.

Study Area and Races

The Pacific Northwest region of the United States and Canada was selected for this study because of the presence of four duathlon race series during the data collection period of May to September 1990. These series offered an excellent chance to study duathlon performance as they attracted many of the same duathletes to their races.

Eight of thirteen duathlon races selected for this study were clustered around Vancouver, British Columbia, and three near Portland, Oregon. Both cities enjoy marine west coast climates with adequate annual precipitation and mild temperatures throughout the year. One of the two additional sites was located on the high plains of eastern Oregon (Helix, Oregon) and the other in the higher, drier

interior of British Columbia (Kamloops, B.C.). Both sites are leeward of the Cascade Mountains, resulting in deficits of atmospheric moisture year-round. The name, location, date, and actual race distances of each duathlon are recorded in Table 1.

Methods

Meteorological Data

Weather data were collected at the start of the race, midpoint, and the race finish. The race start was defined as five minutes before the official race start. For races that contained a 5km run, 30km bicycle, and a second 5km run or distances that closely approximate these, the recording of midpoint weather data took place exactly one hour and fifteen minutes after the first competitors left the starting line. The midpoint recording time was changed to one hour and thirty minutes when bicycle course lengths were ≥ 35 km. The final weather data were recorded as the last person crossed the finish line. This time varied from 35 minutes (Race #1) to one hour and 50 minutes (Race #11) after the midpoint recording. However, most of the final weather recordings were taken one hour and 30 minutes after the midpoint recording.

Weather variables examined include temperature, relative humidity, wind speed, direct radiation, cloud cover, Temperature-Humidity Index, and wind chill. Temperature and relative humidity were recorded using a digital hygrometer

TABLE 1. Location, name, date, and duathlon distance for races used in this study.

Race #	Race Name	Location	Date (1990)	Distances (run#1-bicycle-run#2)
1	Canadian Endurance Series	Langley, B.C.	05/27	3km-20km-3km
2	PTA Rose Festival Biathlon	Hillsboro, Oregon	06/03	5km-30km-5km
3	Prestige Series-Stanley Park	Vancouver, B.C.	06/08	5km-29.7km-5km
4	BC Tel International Duathlon	Victoria, B.C.	06/09	5km-30km-5km
5	Heart of the Country Biathlon	Helix, Oregon	06/16	4.8km-40.2km-3.2km
6	Canadian Endurance Series	Vancouver, B.C.	06/24	5km-40km-5km
7	BC Tel International Duathlon	Whistler, B.C.	07/01	4.5km-32.5km-4.5km
8	PTA Firecracker Biathlon	Wilsonville, Oregon	07/08	5km-30km-5km
9	BC Tel International Duathlon	Kamloops, B.C.	07/15	5.5km-30km-5.5km
10	PTA Midsummer Biathlon	Fairview, Oregon	08/12	5km-30km-5km
11	Prestige Series-Whistler	Whistler, B.C.	09/01	5km-35km-5km
12	Canadian Endurance Series	Vancouver, B.C.	09/08	5km-40km-5km
13	Canadian Endurance Series	North Vancouver, B.C.	09/29	5km-30km-5km

housed inside a standard meteorological shelter. Wind speed was recorded with a digital anemometer. Direct radiation was measured using a solar radiation meter and was estimated to the nearest five W m^{-2} . Cloud cover was a subjective estimate from 0% (no clouds visible) to 100% (sky completely covered). This variable was estimated to the nearest 10% by viewing the sky for approximately two minutes before each recording time. The Discomfort Index (Thom 1959), otherwise known as Temperature-Humidity Index (THI), was used to evaluate the amount of human discomfort felt with the race conditions encountered. Wind chill was calculated using a Standard Wind Chill Equivalent Equation (Dixon and Prior 1987).

Topographic Data

On-site run and bicycle topography data were acquired either before or immediately after each race. A mountain bicycle was ridden over each run course using a cyclocomputer to measure course distance. The type of running surface encountered, path width, and the sinuosity (Mueller 1968) of the course were also recorded. The bicycle course was measured similar to the run course. In addition, topographic maps were used for analyses of run and bicycle course topography. The Earth Resources Data Analysis System (ERDAS) was used to measure race distances and changes in elevation from topographic maps.

Because of scale limitations on available topographic maps (1:50,000 for Canadian maps, 1:24,000 for United States maps), detailed topographic variables could not be calculated for the run courses. Instead, a subjective topographic rank variable (run rank) was devised based on observations taken at the race site. After considering all aspects of course topography and layout (e.g. slope, net gain or loss, sinuosity, running surface), difficult courses were assigned a rank of three, moderate courses a two, and easy courses a rank of one.

Topographic map detail was sufficient for analyzing bicycle course topography. Four variables are used to describe bicycle course topography. Local relief (meters) for this study was defined as the difference in elevation between the highest and lowest points on the bicycle course. These points were read directly from the topographic map(s) or interpolated if they were between two contour lines. Net gain or loss (meters) in the first half of the course was defined as the difference

in elevation between the start and the midpoint of the bicycle course. Average course slope (degrees) was calculated by modifying an existing average slope formula (Wentworth 1930). An undulation ratio was calculated by dividing the digitized bicycle course distance by the straight-line (flat) distance. This ratio provides an estimate of the vertical deviation of a bicycle course compared to a hypothetically flat course.

Performance Data

The variables first run time and second run time were used in their original format. Run disparity was measured as the difference between the first run time and the second run time. The recorded overall and bicycle split times included run/bicycle and bicycle/run transition times (the time used by competitors to change from one event to the next). These transition times were subtracted from the originally recorded bicycle and overall times before any statistical analyses were performed.

Mathematical interpolation was used on race times where course distances did not match the 5km first run, 30km bicycle, 5km second run standard used in this study. This was done to simplify statistical comparisons among races and create a standard for the Scheffe post hoc test. To interpolate, a non-standard race distance was divided by the standard race distance to calculate a standardizing coefficient. A standardized race time for each MMP duathlete was then calculated by multiplying this coefficient by each non-standard race time.

Once linear interpolation was performed on all non-standard races, the average and standard deviation was calculated for the total race population of each race. The MMP sample was taken as any duathlete fitting in a range of plus or minus one standard deviation from the overall race mean. This group of duathletes was used to calculate the average and standard deviation for the first 5km run, 30km bicycle, overall, second 5km run, and 5km run disparity.

Statistical Analyses

MMP average race times, topographic and race-day weather variables were checked for normality. All variables were tested at the 0.05 level of significance. Most variables were normally distributed, with a few exceptions (wind speed) falling between 0.05 and 0.07 level of significance.

Subtraction matrices were constructed using all MMP average race times. These subtraction matrices were used to identify unique races, races that appear to enhance or reduce MMP duathlon performance. A Scheffe post hoc test of ANOVA was performed on all MMP race times, allowing a multiple-comparison of means. The results of each Scheffe test were combined with the subtraction matrix results to simplify analysis. The primary use for the Scheffe test is to validate, statistically, unique races found from the subtraction matrix analysis.

Results and Discussion

MMP sample sizes, average race times and the respective standard deviations for each segment of the races studied are listed in Table 2. A summary of the overall topographic characteristics of each race is provided in Table 3. Topographic profiles of the 30km bicycle courses are shown in Figure 1. Average weather conditions for each race are summarized in Table 4.

First 5km Run Performance

The first 5km run subtraction/Scheffe matrix (Table 5) shows distinct groupings of slower and faster

average performance times. Races #5, #6, #7, #11, #12, and #13 display a significant reduction in run time from the rest of the races. These six races appear to correspond well with their difficult run ranks (run rank = 3) (Table 3). The exception is race #11 (run rank = 2), which was a borderline case between a moderate and difficult ranked course. Races #7 and #11 had similar run courses, both held on mountain trails/roads of gravel. This combination of gravel surface and hills resulted in a reduction in performance compared to races #4 and #9 (Table 5), which were held on flat, paved surfaces. Although there was a large difference in weather conditions (Table 4), races #4 and #9 (both run ranks = 1) had similar race averages. First 5km run performance appears to be more strongly influenced by run course topography than by race-day weather.

Races #6 and #12 are of particular interest because they were held on the same difficult run course (run rank = 3) at different times of the year. No significant difference exists between race #6 and #12 according to results from a Scheffe post hoc test (Table 5). Despite being run under different weather conditions (Table 4), only seven seconds separates the first 5km run segment of these two duathlons (Table 5).

TABLE 2. Mean race times and standard deviation of race time.
Race times in seconds** (standard deviation).

Race # (# of MMP)	Run #1	Bike	Run #2	Overall	Disparity*
1 (n=70)	1219 (114)	3228 (214)	1324 (118)	5663 (362)	105
2 (n=84)	1167 (77)	3243 (169)	1267 (88)	5679 (243)	100
3 (n=226)	1181 (91)	3106 (203)	1282 (108)	5579 (352)	101
4 (n=127)	1121 (84)	3164 (221)	1227 (105)	5511 (347)	106
5 (n=55)	1276 (116)	3671 (354)	1389 (231)	5972 (535)	112
6 (n=71)	1276 (109)	3101 (204)	1475 (159)	5516 (348)	198
7 (n=114)	1312 (95)	3071 (214)	1494 (130)	5647 (362)	183
8 (n=117)	1195 (106)	3219 (233)	1308 (143)	5724 (395)	113
9 (n=62)	1105 (67)	3183 (204)	1205 (82)	5537 (281)	101
10 (n=123)	1235 (98)	3050 (235)	1341 (119)	5626 (388)	107
11 (n=155)	1299 (106)	3191 (228)	1446 (153)	5754 (399)	147
12 (n=66)	1269 (80)	3101 (200)	1435 (150)	5477 (314)	166
13 (n=65)	1283 (91)	3208 (228)	1425 (114)	5920 (382)	142

* First 5km run/Second 5km run disparity calculated from race averages.
** Times for races 1, 3, 5, 6, 7, 9, 11, 12 are interpolated to the international distance (5km run, 30km bike, 5km run).

TABLE 3. Topographic characteristics of individual races.

Race#	Local Relief (meters)	Gain or Loss (meters)	Undulation Ratio	Average Slope (degrees)	Run Rank
1	28.04	-22.86	1.000046	0.47	2
2	88.39	8.53	1.000443	1.33	2
3	55.00	0.00	1.001132	1.20	1
4	23.00	1.00	1.000120	0.32	2
5	146.96	-39.93	1.000439	1.81	3
6	66.04	-31.00	1.000085	0.42	3
7	152.40	-128.02	1.001534	1.75	3
8	73.15	0.00	1.001034	1.39	1
9	33.53	-21.34	1.000047	0.29	1
10	12.51	6.70	1.000001	0.09	2
11	179.83	-167.64	1.001574	1.79	2
12	66.04	-31.00	1.000085	0.42	3
13	25.00	0.00	1.000082	0.30	3

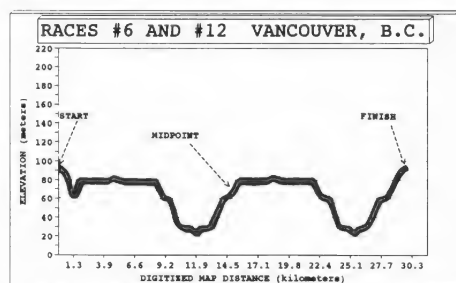
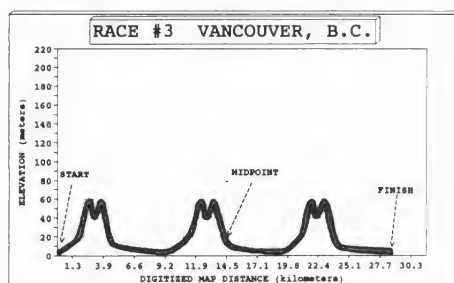
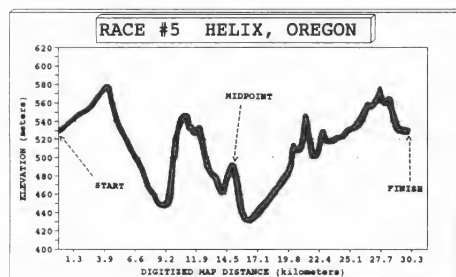
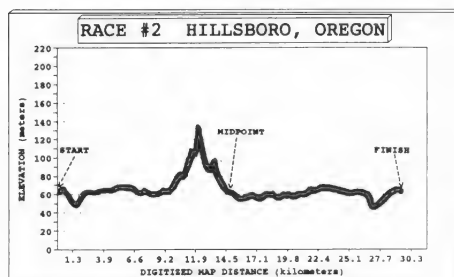
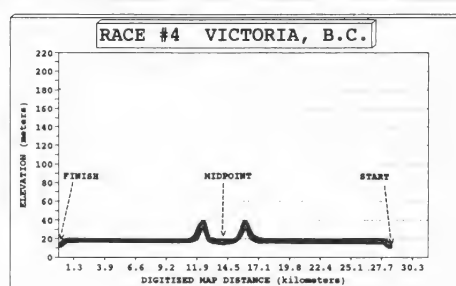
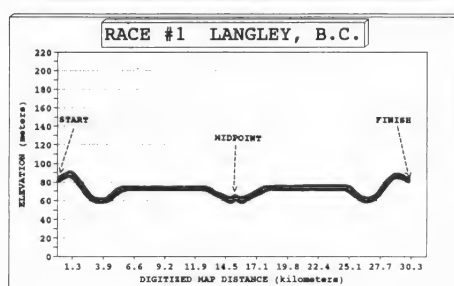


Figure 1A. Bicycle course elevation profile for race #1-6 and race #12. Vertical exaggeration is 80x.

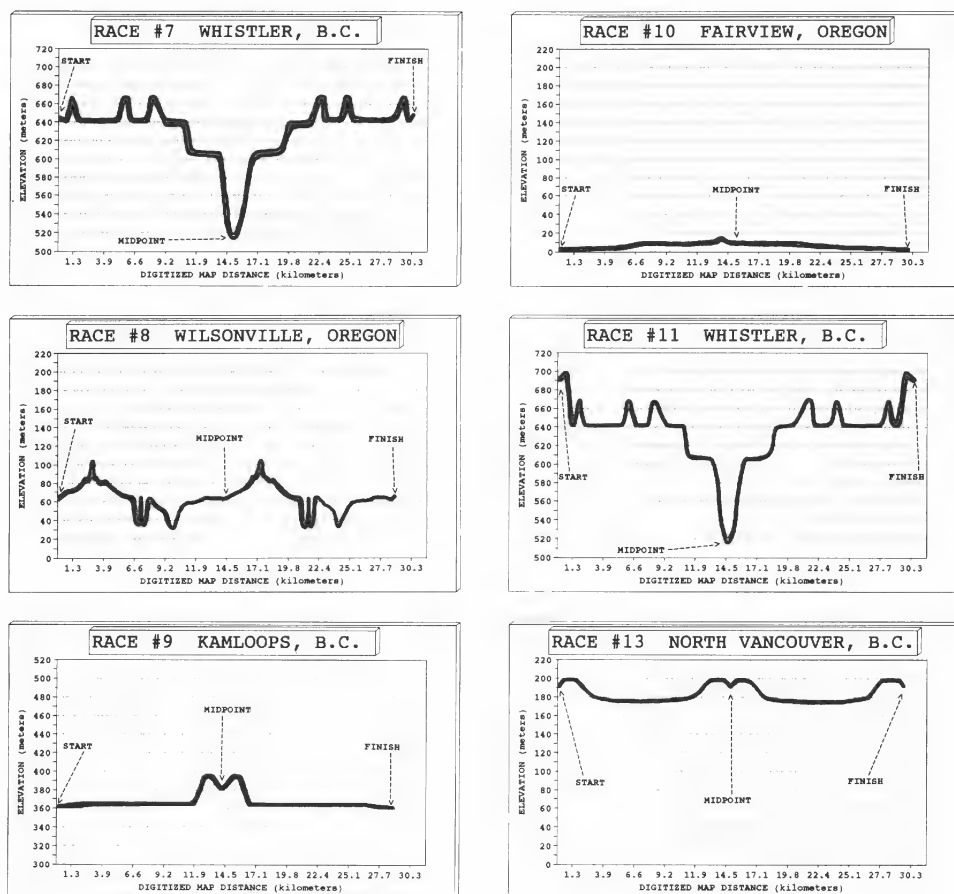


Figure 1B. Bicycle course elevation profile for race #7-11 and race #13. Vertical exaggeration is 80x.

TABLE 4. Mean weather conditions recorded at each race.

Race#	Temperature °C	Relative Humidity (%)	Wind Speed m sec ⁻¹	Direct Radiation W m ⁻²	Cloud Cover (%)	Temp-Humidity Index (THI)	Wind Chill
1	15.19	78.67	0.43	275.00	100.00	15.05	14.38
2	16.11	73.00	1.92	580.00	80.00	15.80	12.54
3	13.70	91.33	0.00	181.67	100.00	13.72	13.70
4	10.00	82.67	1.47	413.33	93.33	10.38	7.27
5	20.00	45.33	5.17	1013.33	30.00	18.20	10.37
6	20.00	58.00	0.40	290.00	36.67	18.60	19.25
7	14.63	63.33	0.05	566.67	86.67	14.50	14.54
8	23.33	54.67	0.40	980.00	10.00	21.01	22.59
9	26.11	29.67	0.50	996.67	0.00	21.43	25.18
10	22.78	66.00	1.42	925.00	6.67	21.14	20.14
11	11.85	77.00	0.00	218.33	10.00	12.12	11.85
12	17.04	71.67	0.42	216.67	10.00	16.56	16.26
13	16.11	68.33	0.38	485.00	66.67	15.74	15.40

TABLE 5. Subtraction and yes/no matrix for MMP first 5km run performance. The difference in average race times is given in seconds. "Y" indicates a significant difference between race means at the 0.05 level of confidence based on a Scheffe post hoc test.

		R A C E #												
		1*	2	3	4	5*	6	7*	8	9*	10	11	12	13
	Time (sec.)	1219	1167	1181	1121	1276	1276	1312	1195	1105	1235	1299	1269	1283
1*	1219	—	51	38(Y)	98	-57	-57	-93(Y)	24	114(Y)	-16	-80(Y)	-50	-64
2	1167		—	-14	46	-109(Y)	-109(Y)	-109(Y)	-28	63	-67(Y)	-132(Y)	102(Y)	-115(Y)
3	1181			—	60(Y)	-95(Y)	-95(Y)	-130(Y)	-14	77(Y)	-54(Y)	-118(Y)	-88(Y)	101(Y)
R 4	1121				—	-155(Y)	-155(Y)	-191(Y)	-74(Y)	16	-114(Y)	-178(Y)	-148(Y)	-162(Y)
A 5*	1276					—	0	-36	81(Y)	171(Y)	41	-23	7	-7
C 6	1276						—	-35	81(Y)	172(Y)	42	-23	7	-6
E 7*	1312							—	116(Y)	207(Y)	77(Y)	13	43	29
# 8	1195								—	91(Y)	-39	-104(Y)	-74(Y)	-87(Y)
9*	1105									—	-130(Y)	-194(Y)	-164(Y)	-178(Y)
10	1235										—	-64(Y)	-34	-48
11	1299											—	30	16
12	1269												—	-14
13	1283													—

* indicates the race time was interpolated to the international (5km-30km-5km) distance

30km Bicycle Performance

Two races (#2 and #5) have a distinctly different pattern from the rest of the races (Table 6). These two races possessed the two highest average wind speeds (Table 9), had topographically challenging course designs (Figure 1A), and had the slowest average race times (Table 6). A main factor in reducing 30km bicycle performance for race #2 appears to be the challenging hill near the midpoint (Figure 1A). The undulating course and midpoint wind speed of 2.50m sec^{-1} also likely contributed to the reduction in performance. Besides a challenging first half, race #5 had a long continuous climb for the cycling duathlete from the midpoint almost to the start/finish area (Figure 1A). The long, challenging climbs of race #5 coupled with the midpoint wind speed (5.90m sec^{-1}) account for the large reduction in performance compared to other races (Table 6).

The fastest average 30km bicycle times for MMP duathletes are found on a variety of course designs. The topographic analysis (Table 3) and course profile (Figure 1B) suggest that race #10 had the fastest average 30km bicycle time because of a lack of topographic variability. In contrast, race #7 was perceived as a difficult course by du-

athletes, and this is backed by the topographic analysis of the course (Table 3). However, the second fastest bicycle time (Table 6) was recorded in race #7. The key to the fast average time appears to be net loss (-128m) in the first half of the course (Figure 1B). This large drop in elevation resulted in high racing speeds, allowing duathletes to perform at or above their capabilities for the first half of the course and negating the reduction in performance caused by the long climb back to the transition area. Race #11 used the same course as race #7 but included an extension onto the start (Figure 1B) that accounts for the longer actual (versus interpolated) distance. The result was a slower average race time for race #11.

Races #6 and #12 are of particular interest because they used the same bicycle course at different times of the year. Although there were differences in average weather conditions between race #6 and #12 (Table 4), with race #6 having a greater potential for heat stress, average race times for the two races are identical (3101 seconds). This represents a tie for the third fastest time among races sampled (Table 6). A small local relief, average slope, and a loss in elevation in the first half of the course contribute to the fast race times. Large losses in elevation in each loop

TABLE 6. Subtraction and yes/no matrix for MMP 30km bicycle performance. The difference in average race times is given in seconds. "Y" indicates a significant difference between race means at the 0.05 level of confidence based on a Scheffe post hoc test.

		R A C E #												
		1*	2	3*	4	5*	6*	7*	8	9	10	11*	12*	13
	Time (sec.)	3228	3243	3106	3164	3671	3101	3071	3219	3183	3050	3191	3101	3208
1*	3228	-	-15	122	64	-443(Y)	127	157(Y)	8	45	178(Y)	37	127	20
2	3243		-	138(Y)	80	-427(Y)	142	172(Y)	24	60	194(Y)	52	143	35
3*	3106			-	-58	-565(Y)	4	34	-114	-78	56	-86	5	-103
R	4	3164			-	-507(Y)	63	93	-56	-19	114	-28	63	-44
A	5*	3671				-	569(Y)	599(Y)	451(Y)	487(Y)	621(Y)	479(Y)	570(Y)	462(Y)
C	6*	3101					-	30	-118	-82	51	-90	1	-107
E	7*	3071						-	-148(Y)	-112	21	-120	-29	-137
#	8	3219							-	36	170(Y)	28	119	11
	9	3183								-	133	-8	83	-25
	10	3050									-	-142(Y)	-51	-158(Y)
	11*	3191										-	91	-17
	12*	3101											-	-108
	13	3208												-

* indicates the race time was interpolated to the international (5km-30km-5km) distance

of this two loop course (Figure 1A) enabled MMP duathletes to perform at or above their capabilities.

Second 5km Run Performance

The effects of run course difficulty (run rank) should become more significant after running and bicycling a total of 35km. The difference between difficult (run rank = 3) and easy (run rank = 1) courses is evident when looking at the subtraction matrix (Table 7). Second 5km run times for races #4 and #9 were the two fastest. The fast times are most likely related to the lack of difficulty in the preceding bicycle courses. Races #6, #7, #11, #12, and #13 show pronounced decreases in average run performance compared to races #4 and #9. Again, this appears to be primarily a function of the difficulty of these five run courses. Results from the Scheffe post hoc test (Table 7) support the findings from the subtraction matrix, as almost all race pairs having second 5km run time differences of greater than ± 94 seconds were significantly different at the 0.05 level. Second 5km run performance may be the best indicator of overall course difficulty. The assumption is that slower second 5km run times equate to a more difficult first run and/or 30km bicycle course experienced by the MMP duathlete.

Overall Performance

The apparent overall homogeneity among courses leads to a lack of usefulness when using overall race times to analyze performance. Although differences exist between the individual segments of each race, the resulting average overall race times are similar. For example, duathletes ran fast on the easy run course of race #4 but much slower for race #6, a difficult run course. In contrast, duathletes cycled the fastest on the bicycle course for race #6 while race #4 saw an intermediate time for MMP duathletes. Although the individual segments of each course contain different physical characteristics, the final overall race averages are approximately equal (Table 2).

Races #5 and #13 display the only unique patterns (Table 8). Except for wind speed, average weather conditions were not largely different between the two races (Table 4). Both races had difficult run and bicycle segments to their respective courses (Table 3). The small difference between the two races can be accounted for by the more difficult bicycle course in race #5 (Figure 1A). The rest of the overall race times are clustered around 5500 seconds. Thus, examination of overall race times contributes little to the knowledge of the effects of weather and course topography on MMP duathlete performance.

TABLE 7. Subtraction and yes/no matrix for MMP second 5km run performance. The difference in average race times is given in seconds.
 "Y" indicates a significant difference between race means at the 0.05 level of confidence based on a Scheffe post hoc test.

R A C E #														
	1*	2	3	4	5*	6	7*	8	9*	10	11	12	13	
	Time (sec.)	1324	1267	1282	1227	1389	1475	1494	1308	1205	1341	1446	1435	1425
1*	1324	-	56	42	97(Y)	-65	-151(Y)	-171(Y)	15	118(Y)	-18	-122(Y)	-111(Y)	-101
2	1267		-	-14	41	-121(Y)	-207(Y)	-227(Y)	-41	62	-74	-178(Y)	-167(Y)	-157(Y)
3	1282			-	-85	-324(Y)	-186(Y)	-382(Y)	-126	-125	-264	-360(Y)	-242(Y)	-280(Y)
R 4	1227				-	-162(Y)	-248(Y)	-268(Y)	-82(Y)	21	-115(Y)	-219(Y)	-208(Y)	-198(Y)
A 5*	1389					-	-86	-106(Y)	80	183(Y)	47	-57	-46	-36
C 6	1475						-	-20	166(Y)	269(Y)	133(Y)	29	40	50
E 7*	1494							-	186(Y)	289(Y)	153(Y)	49	60	70
# 8	1308								-	103(Y)	-33	-137(Y)	-126(Y)	-116(Y)
9*	1205									-	-136(Y)	-240(Y)	-229(Y)	-219(Y)
10	1341										-	-104(Y)	-94(Y)	-83
11	1446											-	11	21
12	1435												-	10
13	1425													-

* indicates the race time was interpolated to the international (5km-30km-5km) distance

TABLE 8. Subtraction and yes/no matrix for MMP overall performance. The difference in average race times is given in seconds.
 "Y" indicates a significant difference between race means at the 0.05 level of confidence based on a Scheffe post hoc test.

		R A C E #												
		1*	2	3*	4	5*	6*	7*	8	9*	10	11*	12*	13
	Time (sec.)	5663	5679	5579	5511	5972	5516	5647	5724	5537	5626	5754	5477	5920
1*	5663	-	-16	84	152	-309(Y)	147	16	-61	126	37	-91	186	-257
2	5679		-	100	167	-293(Y)	163	32	-45	142	53	-75	202	-241
3*	5579			-	68	-393(Y)	63	-68	-145	42	-47	-175	102	-341(Y)
R 4	5511				-	-460(Y)	-5	-135	-212	-26	-115	-242(Y)	34	-408(Y)
A 5*	5972					-	456(Y)	325	248	435(Y)	346(Y)	218	494(Y)	52
C 6*	5516						-	-131	-207	-21	-110	-238	39	-404(Y)
E 7*	5647							-	-77	110	21	-107	169	-273(Y)
# 8	5724								-	186	98	-30	246	-196
9*	5537									-	-89	-217	60	-383(Y)
10	5626										-	-128	149	-294(Y)
11*	5754											-	276(Y)	-166(Y)
12*	5477												-	-442(Y)
13	5920													-

* indicates the race time was interpolated to the international (5km-30km-5km) distance

TABLE 9. Subtraction and yes/no matrix for MMP first and second 5km run disparity. The difference in average race times is given in seconds. 'Y' indicates a significant difference between race means at the 0.05 level of confidence based on a Scheffe post hoc test.

		R A C E #												
		1*	2	3	4	5*	6	7*	8	9*	10	11	12	13
	Time (sec.)	105	100	101	106	112	198	183	113	101	107	147	166	142
1*	105	-	5	4	-1	-7	-93(Y)	-78(Y)	-8	4	-2	-42	-61	-37
2	100		-	-0	-6	-12	-98(Y)	-83(Y)	-13	-1	-6	-46	-66(Y)	-42
3	101			-	-5	-12	-98(Y)	-82(Y)	-13	-0	-6	-46(Y)	-65(Y)	-41
R 4	106				-	-7	-93(Y)	-77(Y)	-7	5	-1	-41	-60(Y)	-36
A 5*	112					-	-86(Y)	-70(Y)	-1	12	6	-34	-53	-29
C 6	198						-	16	85(Y)	98(Y)	92(Y)	52	33	57
E 7*	183							-	69(Y)	82(Y)	76(Y)	36	17	41
# 8	113								-	12	7	-33	-53	-29
9*	101									-	-6	-46	-65	-41
10	107										-	-40	-59(Y)	-35
11	147											-	-19	5
12	166												-	24
13	142													-

* indicates the race time was interpolated to the international (5km-30km-5km) distance

5km Run Disparity

Results suggest that races #6, #7, and #12 are significantly different from the other races (Table 9). There appears to be two distinct groupings for MMP duathlete 5km run disparity. One group displays large differences (>142 seconds) between first and second 5km runs (races #6, #7, #11, #12, #13). The remaining races are clustered around a smaller disparity of about 100 seconds (Table 9). These two groupings are evident on the subtraction matrix of raw data (Table 9). Although there are large 5km run disparities for races #11 and #13, the Scheffe post hoc test was unable to reveal any unique statistical patterns when compared to the other races. However, the subtraction matrix shows these races differ by as much as 57 seconds from the other races (Table 9). Most duathletes consider a reduction of 142 seconds (2 minutes and 22 seconds) and 147 seconds (2 minutes and 27 seconds) in 5km run performance substantial.

Conclusions

The focus of this study was on the relationship between performance in male athletes during duathlon events and the suite of topographic and weather conditions encountered at each race. Subtraction matrices and a series of Scheffe post hoc tests of ANOVA were used to identify unique races and race patterns. Aspects of race-day weather and topographic variability were examined in conjunction with the matrices to help explain MMP performance among the duathlon races. The findings suggest: 1) first 5km run times are primarily affected by run course topography, 2) 30km bicycle times are similar among races except those with large amounts of topographic variability or high wind speeds, 3) poor second 5km run performance is due largely to a combination of run and bicycle course difficulty, 4) 5km run disparity may be the best indicator of overall course difficulty as second 5km race times drop considerably following a difficult first 5km run and/or 30km bicycle course, and 5) other than wind speed, weather conditions have little influence on duathlon performance during the summer months in the Pacific Northwest.

Literature Cited

- Costill, D. L. 1972. Physiology of marathon running. *Journal of the Amer. Med. Assoc.* 221:1024-1029.
- Davies, C. T. M. 1980. Effects of wind assistance and resistance on the forward motion of a runner. *J. of Appl. Physiology* 48:702-709.
- Dixon, J. C., and M. J. Prior. 1987. Wind-chill indices—a review. *Meteor. Mag.* 116:1-17.
- England, A. C. III, D. W. Fraser, A. W. Hightower, R. Tirinnanzi, D. J. Greenberg, K. E. Powell, C. M. Slovis, and R. A. Varsha. 1982. Preventing severe heat injury in runners: suggestions from the 1979 Peachtree road race experience. *Ann. of Internal Med.* 97:196-201.
- Eyton, J. R. 1987. Morphometrics of the Chasquis Invitational Rocky Mountain Road Race. *Sport Place* 1:39-47.
- Graham, R. 1990. State of the sport-Triathlete magazine ponders the triathlon: its current health and hopes for the future. *Triathlete* 80:32-48.
- Hiller, W. D. B. 1989. Dehydration and hyponatremia during triathlons. *Med. and Science in Sports and Exercise* 21:219-220.
- Hiller, W. D. B., M. L. O'Toole, E. E. Fortress, R. H. Laird, P. C. Imbert, and T. D. Sisk. 1987. Medical and physiological considerations in triathlons. *The Amer. J. of Sportsmedicine* 15:164-167.
- Knowlton, R. G., Ackerman, K. A. and L. A. Kaminsky. 1988. Physiological and performance comparisons of running flat and hill routes as applied to orienteering navigation. *J. of Sports Med. and Physical Fitness* 28:189-192.
- Kohrt, W. M., Morgan, D. W., Bates, B. and J. S. Skinner. 1987. Physiological responses of triathletes to maximal swimming, cycling, and running. *Med. and Science in Sports and Exercise*. 19:51-55.
- Kreider, R. B., T. Boone, W. R. Thompson, S. Burkes, and C. W. Cortes. 1988. Cardiovascular and thermal responses of triathlon performance. *Med. and Science in Sports and Exercise* 20:385-390.
- Loftin, M., B. L. Warren, S. Zingraf, J. E. Brandon, J. E. Skuldt, A. Skuldt, and B. Scully. 1988. Peak physiological function and performance of recreational triathletes. *J. of Sports Med. and Physical Fitness* 28:330-335.
- Mueller, J. E. 1968. An introduction to the hydraulic and topographic sinuosity indexes. *Ann. of the Assoc. of Amer. Geog.* 58:371-385.
- Newkirk, G. 1989. Biathlons take off—a survey of 1989's best biathlons. *Triathlete* 68:38-55.
- Pugh, L. G. C. E. 1974. The influence of wind resistance in running and walking and the mechanical efficiency of work against horizontal or vertical forces. *J. of Physiology* 213:255-276.
- Thom, E. C. 1959. The Discomfort Index. *Weatherwise* 11:57-60.
- Wentworth, C. K. 1930. A simplified method of determining the average slope of land surfaces. *Amer. J. of Science* 20:184-194.

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Book Review

Wildlife Management and Subsistence Hunting in Alaska. Henry P. Huntington. University of Washington Press. \$50.00. 172 pp.

Henry P. Huntington's study centers on the emerging fact, in his view, that management of local subsistence hunting (primarily by Iñupiat Eskimos) in northern Alaska is inadequate and often ineffectual. Huntington spent two years (1988-1990) working for the North Slope Borough of Wildlife Management in Barrow, Alaska; his study methods included examining the written records of management agencies and regimes, interviewing people involved in management planning and administration, and participant observation with local hunters. Under current management regimes and regulations, local hunters are often unable to legally provide for their "nutritional, cultural, or spiritual needs or to continue customary patterns of resource use"—even when animal populations are at high levels. Not surprisingly, this has led to widespread disregard of bag limits, licensing laws, and other regulations on the part of subsistence hunters, as they pursue what they consider their rightful claims to Alaskan wildlife. Huntington's study (essentially, his doctoral dissertation) examines current management and regulatory regimes specific to northern Alaska, focusing primarily on one aspect of management—the "interaction between the regime and local subsistence hunters." Huntington does not intend to provide extensive suggestions for changing existing regimes. Rather, his objective is to identify "characteristics shared by effective regimes." Drawing on these characteristics, he offers a list of evaluative criteria as a new means of analyzing and understanding existing and proposed management, and concludes with an endorsement of the cooperative management approach.

Huntington defines "effective management" narrowly: that which protects animal populations and allows local people to provide for their needs. On the other hand, Huntington expands the definition of local need to include cultural context. Local need is a "nutritional, cultural, or spiritual requirement that cannot be readily or adequately replaced." Cultural needs centering on animals or animal products may be as important to subsistence

hunters as bagging game; rarely is wild meat needed to avoid outright starvation.

As an intellectual point of departure, Huntington provides a brief summary of the origins of American game laws and wildlife management, beginning with the era of the Norman Conquest in England, to the reaction to English game laws in early America, and finally, to the establishment of game laws and regulations in the state of Alaska. Huntington's salient points are first, that formal regulation of hunting began in response to the "pressures and needs" of sport hunters and, therefore, that many management techniques (e.g., seasons and individual bag limits) are more suitable to recreational hunting than to subsistence use. Second, American game laws and management traditions, guaranteeing equal rights for all hunters, evolved in reaction to English tradition, which reserved hunting privileges for a wealthy elite. This last fact is particularly relevant to Huntington's continuing discussion of the Alaska National Interest Lands Conservation Act (ANILCA) (1980), which granted subsistence (including hunting) privileges to rural residents residing in and around newly formed federally managed protected areas. Huntington observes that "to the extent that a subsistence priority creates a new privileged class of users, it runs counter to the egalitarian basis of American game laws."

Huntington also provides a short history of customs and patterns of wildlife use of northern Alaska's Iñupiat, beginning with the archeological record and ending with a discussion of current subsistence patterns. Topics of discussion include commercial whaling, reindeer herding, fur trapping, the Alaska Native Claims Settlement Act (1980) and newly realized oil wealth. The northern Alaska Iñupiat developed a culture which is characterized by interdependence and cooperation, yet also highly individualistic. Despite extensive contact with outsiders and adoption of Western technology, subsistence hunting remains central to individual Iñupiat identity, and the sharing of subsistence harvest is important communally. Moreover, subsistence resources remain essential to the region's economy despite the fact that oil wealth has created considerable prosperity for many individuals and unprecedented wealth for local governments.

Huntington devotes five chapters to examining management regimes of federal, state, and local governments, as well as the alternative approach of cooperative management. He reviews current regimes with the goal of deriving effective management criteria, ending each chapter with a list of evaluative criteria characterizing the features shared by successful regimes. The federal government is responsible for the management and regulation of federal lands, marine mammals, migratory birds, and for mineral resources on government land and on the outer continental shelf. The federal government has also regulated subsistence on its lands since the McDowell decision (1989), which found ANILCA incompatible with the state constitution's guarantee of equal access to subsistence resources for all Alaskans. In all, five federal agencies and seven international treaties are involved in managing and regulating wildlife use in northern Alaska. As a result, Huntington observes, "federal management of wildlife resources in northern Alaska is piecemeal at best." He believes, however, that the mechanisms for producing effective management are already present in federal agencies.

In examining state management, Huntington notes that prior to the McDowell decision, the state had singular authority to regulate hunting; now, however, the federal government regulates subsistence hunting on its own lands (approximately 65% of Alaskan land). He believes the Alaska Department of Fish and Game has done an impressive job of collecting subsistence use data, enabling that agency to be the "best informed advocate for subsistence uses"; however, the State's hunting regulations remain largely ignored by local hunters and widely criticized as ineffectual.

At the core of this dissension lie the very real differences between subsistence hunting and recreational hunting. Huntington reminds us that subsistence hunting, with its sole practical goal of providing food, favors the most efficient forms of human predation and may have little use for the aesthetic or abstract concerns of hunting sportsmanship (e.g., more humane killing techniques). The subsistence hunter, motivated by the need to acquire food and other animal products with minimum energy expenditure, may feel justified in using whatever means accomplishes this goal. This may include incorporating modern technology (such as snowmobiles) with the more customary aspects of the hunt. Given this motivational context, state laws which require hunters to pursue

animals on foot, or which forbid the use of certain weapons, can seem inappropriate or simply irrelevant. Bag limits expose a similar gap between state regulation and subsistence reality. To a subsistence hunter, the individually designated bag limit may seem unfair and, in fact, neglectful of local needs centering on family or village requirements. Consequently, few Iñupiat obtain hunting licenses or report animal harvest. Huntington believes that substantial changes are needed to the state system's regulatory requirements and management practices in order to answer the needs of northern Alaskans.

Regarding local government, Huntington looks at the several management regimes deployed in North Slope Borough. Lacking regulatory authority, the Borough's local government promotes wildlife programs through a Department of Wildlife Management, a Science Advisory Committee and a Fish and Game Management Committee; these organizations conduct research, perform reviews to insure that the research reflects local needs, and link villagers with managers and researchers through village representatives, respectively. Although the Borough's resource-rich wealth makes its case unique (and perhaps difficult for other communities to emulate), Huntington feels that wildlife managers seeking improved programs would benefit from examining its successful innovations closely.

The final regime Huntington examines is cooperative management (or "co-management"), an alternative approach which arose from the need to effectively negotiate the differences between Western wildlife management regimes and the needs of indigenous people. The central concept of this approach is to include local residents in the management process, thereby promoting better understanding and cooperation on both sides. Local people would have more opportunity to offer their perspectives, and in this way could influence management decisions; managers would get better harvest data and higher rates of compliance with regulations. In theory, both sides benefit. Huntington reviews six cooperative management regimes of northern Alaska, concluding that "cooperative regimes have shown themselves on the whole better able to provide effective management of subsistence hunting." In his view, this is because they are 1) effectively focused, since they are usually oriented towards a specific problem and 2) more receptive and adaptable to the needs of subsistence hunters than government management regimes.

Drawing on the characteristics of the successful regimes reviewed, Huntington advances eight criteria to "facilitate successful interaction between a management regime and local subsistence hunters." "Interaction" takes two forms; contact, such as advisory councils and public meetings, and provisions of the management systems, such as regulations and research. These criteria include the following: the regime must be legal (see McDowell decision, above), culturally appropriate, adaptable to local concerns and changes, and include local hunters in all phases of its activity. The regime must also be able to implement its provisions; Huntington explains this final criterion by observing that "legal authority would seem to have little relevance. Instead this ability is a combination of a sense of ownership and in the regulatory provisions, a belief in the relevance of those provisions, and the desire to achieve goals that are shared by hunters and managers."

Using these criteria, Huntington analyzes ten management regimes (including several cooperative management regimes) and rates these regimes with a four-point response format ranging from "very good" to "poor," with the additional option of scoring criteria as "not applicable." Five analyses of regimes by animal species hunted are also provided. Striking differences emerge in the outcomes of the regimes analyzed. For example, Huntington considers migratory bird treaties "culturally inappropriate" and among the least effective management regimes in northern Alaska. "The only point in their favor," he concludes, "is that they are not enforced." Also unsatisfactory is the Marine Mammal Protection Act of 1972 (MMPA), which allows for unrestricted Native harvest of stocks that are not depleted, but forbids non-Native local hunters from hunting these animals altogether. The MMPA "is not particularly relevant to the ecology of marine mammals. . . . [and] has failed to resolve problems of appropriate use and sustainable harvests." To improve walrus management, for example, the regime should consider the strong monetary incentive for harvesting walruses for ivory alone; however, the MMPA deals with this aspect only in a very limited way.

ANILCA receives a mixed grade from Huntington. Despite some successes, this legislation "has not lived up to its promise. In part this is because the agencies responsible for implementing have not carried out the intent of the Act." In addition, Huntington contends that ANILCA itself has inherent

management problems. He considers advisory councils culturally inappropriate in northern Alaska; moreover, the Act does not make explicit the way in which regulations will be created from, or modified by, local people's input.

In contrast, the Yukon-Kuskokwim Delta Goose Management Plan "has no weak spots." "It is the only regime with population thresholds to determine management responses, so that all parties know . . . what responses will be The plan is ecologically relevant and is designed to benefit all users of geese. A substantial effort has been made to inform local residents about the plan and its goals and to involve local people." The plan has succeeded in getting cooperation from Native hunters of the Yukon-Kuskokwim Delta, as well as sport hunters from California. Despite a lawsuit filed (and won) by Alaska sport hunters protesting the plan's allowance of spring geese hunting—on the grounds that the plan violated violation of the migratory bird treaty with Canada—the management plan continues to be a success.

Huntington concludes his study with an endorsement for cooperative management, arguing that future management effectiveness depends upon the cooperation and involvement of local hunters. While he does not consider cooperative management a panacea and also acknowledges the legal barriers to delegating authority to cooperative management systems, Huntington believes that this approach ensures responsiveness to local concerns and instills in local hunters a sense of ownership in the regime.

Huntington capably defines his inquiry and confines his discussion to the stated objectives. The result is a very narrow focus on effective management defined on the basis of interaction with Native local hunters in northern Alaska. For a dissertation, such a limited approach is appropriate. However, this constraint limits the applicability of the study to a nonacademic world that is not so simple. For example, as Huntington recognizes, most agencies have multiple constituencies. Moreover, legal barriers and budget limitations can stand in the way of practicing cooperative management. Finally, not all rural communities having subsistence privileges in Alaska are Native; some community members may be of European descent. The current critical need is for analytical discussion which addresses improving interaction with local hunters, where the various interested parties are considered in realistic legal and political

contexts, and the definition of "effective management" is not exclusively confined to one of the parties.

While Huntington's methods are empirical, they are not scientific. In fairness, Huntington does not claim his discussion is scientific; nevertheless, his explanation of the methods section (only one paragraph long) is deficient for academic readers. Records were examined. What does this mean? How were they examined? Interviews were conducted. What questions were asked, and how were these data analyzed? How might we replicate the study? These are crucial questions if the valuative criteria are to be accepted as holistic and the critical comments as sound. For example, it is one thing to say that the valuative criteria were derived from data collected from structured interviews where both managers and local hunters were carefully sampled and asked questions specifically designed for identifying such criteria. It is very different to say that the criteria are the author's considered opinions after qualitative interviews with several people selected on the basis of opportunity. Or consider the statement that local advisory groups established by ANILCA are "culturally inappropriate." Is this assertion supported by quantitative survey data describing local perceptions? Is it Huntington's opinion after reviewing anthropological accounts of Native culture based on general qualitative descriptions of local culture?

A primary objective of the book is to identify characteristics shared by effective regimes. However, because an operational definition of an effective regime is never provided, the reader cannot know how the writer recognizes an effective regime when he encounters one. The failure to link conclusions to the methods and data collected represent a serious shortcoming of the book. Overall, these problems lead to assertions without sufficient justification. For example, Huntington claims that

the agencies responsible for implementing ANILCA have not attempted to do so. No specific evidence is offered, nor is there any attempt to discriminate between the several federal agencies involved.

Huntington's conclusions concerning the need for cooperative management to achieve effective management are true almost by definition—given his definition of effectiveness. In this study, effective management is built solely around two objectives: 1) managing the wildlife population and 2) meeting the needs of local people. There is no practical or methodological reason to approach the concept of effective management in such narrow terms—even if the focal point of the research is local needs. A more realistic, and ultimately more useful, definition of effective management would address the presence (and simultaneous satisfaction) of multiple objectives and stakeholders.

Despite these shortcomings, Huntington covers a lot of ground and provides a broad and interesting introduction to a complex, controversial subject. The critique of existing management regimes will provide fundamental insights to those less familiar with this situation. Huntington's valuative criteria should prove useful to managers and policymakers as points of departure in considering effective ways of interacting with local people. Local hunters will find helpful testimony in their arguments for more cooperative approaches. For researchers, Huntington's valuative criteria and assertions provide direction for future studies in this area, particularly concerning quantitative policy analysis.

—Darryll R. Johnson
National Biological Survey
Cooperative Park Studies Unit
College of Forest Resources AR-10
University of Washington
Seattle, Washington 98195

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